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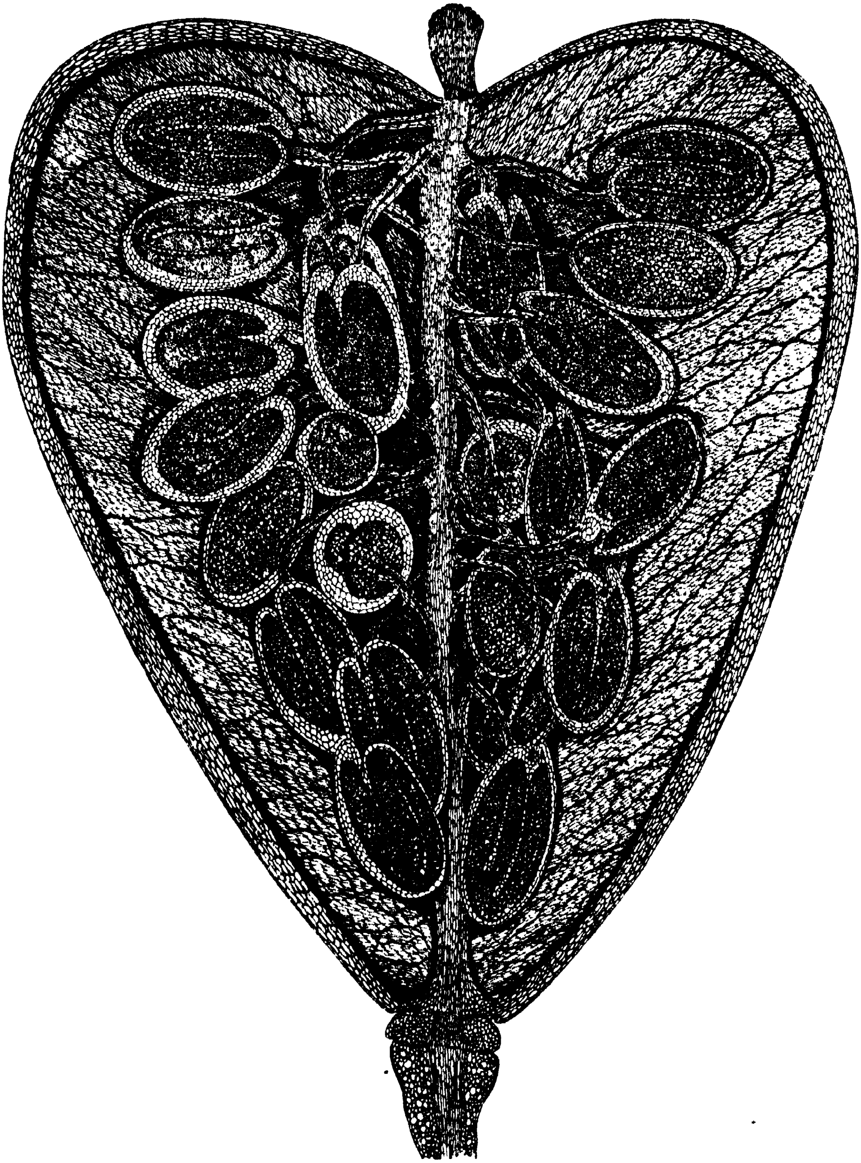

The silicular fruit of Shepherd's Purse (*Capsella Bursa-pastoris*). Cleared in Eau-de-Javelle and stained in bulk with Eosin.

Frontis.

INTRODUCTION TO FLORAL MECHANISM

BY

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PREFACE

The present volume is intended as an introduction to the study of the structure, development and functions of the flower. The subject-matter forms a course in Floral Morphology which it is hoped will be found suitable for sixth-form pupils and students in technical colleges, as well as for the first-year university students for whom the course was originally drawn up. In view of the increasing prominence now given to Cytology and Genetics in Botany it has been thought advisable to provide the elementary student with some introductory knowledge bearing on the application of Cyto-Genetics to Heredity, Hybridization and Plant Breeding. An attempt has therefore been made to consider the flower as a mechanism of inheritance and thus to interweave the main principles of these newer sciences. An account of the development of the gametic cells follows in natural sequence, and this is succeeded by a brief discussion of the technique and results of plant hybridization.

Though nothing has been more inspiring in the advances of recent years than the growing insight into the genetical affinities that exist between plants hitherto regarded as distinct in their relations, the data are still insufficient as a basis for a revised classification of the Angiosperms. The arrangement of a selected number of Families of Flowering Plants outlined in Chap. XIV is, therefore, not intended to convey any evolutionary sequence, but is included as an introduction to the use of a Flora.

The book is divided into two parts for convenience; in actual practice in the laboratory, development and floral structure are studied concurrently. The selected types are all common wild or easily accessible cultivated plants. The usual procedure in class-work is that of flower dissection followed by a large-scale drawing of the median section; with some of the smaller types, drawings of detached parts are also shown; in all cases a floral diagram and a floral formula are included. With the exception of figs. 26 and 46 (C, D) all the illustrations are from original drawings by the author. While it has not been the aim of the author to make these drawings elaborate, he feels that the student should see more of the developmental and anatomical aspect of the subject than is usually supplied in the elementary text-book. An attempt has therefore been made to induce the student to treat the flower in the same way as he deals with the root, stem, and leaf. Even inflorescence schemes and floral diagrams come to have a real meaning if their skeletons can be seen clothed with flesh!

The writer wishes to thank Professor Walton and his colleagues in the Department of Botany, University of Glasgow; Dr. John Thomson, Adviser of Studies, University of Glasgow; Professor Montagu Drummond; Dr. Blodwen Lloyd, Royal Technical College, Glasgow; and Mr. G. H. Banks, Botanic Gardens, Glasgow, for their help and suggestions. He is also indebted to Professor C. W. Wardlaw, University of Manchester, for the use of microscopic slides, from which several illustrations in Part I were made; and to Professor Sir George Stapledon and his staff for permission to describe the work and organization of the Welsh Plant Breeding Station, Aberystwyth. Thanks are due to Professor A. K. White, M.A., University of Johannesburgh; Mr. Angus Macdonald, M.A., H.M.I., Kilmacolm; and Mr. W. Rennie, Glasgow, who as interested readers have been of great help to the author.

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PART I

CHAPTER I

The Flower

The Flowering Plants or Angiosperms are the dominant types of the plant kingdom to-day. Their world-wide distribution in all habitats is striking evidence of their adaptability to the environment and of their success in the struggle for existence.

Comparative study of plants representative of all classes of the vegetable kingdom shows that they are the most highly differentiated in vegetative development and functions. Moreover, the reproductive mechanism finds its highest organization in the flower, and propagation its most successful means in the seed of the Angiosperm.

After a period of vegetative activity during which the individual develops root, stem and leaves for purposes of nutrition and storage of food, the flowering plant proceeds to the sexual phase or formation of spores. The function of the flower is to produce the spores, namely the pollen (male) and ovules (female); after fertilization by the pollen the ovules become seeds.

An important preliminary to fertilization in the Angiosperm is the conveyance of pollen to a special part of the flower, namely, the carpel, which encloses the ovules. (Hence the term " angiosperm " for a plant having its " seeds enclosed in a vessel ", here, the carpel.) Pollination may be carried out through the agency of wind or insects.

The great variety and endless modifications of floral structure are undoubtedly associated with pollination which attains its highest precision through the aid of insects. There is, moreover, strong evidence in support of the conclusion that pollination by insect agency has played an important part in the evolution and elaboration of floral mechanism.

The functions of the flower after fertilization are not complete until the carpel and its ovules are converted into fruit and seeds. The infinite variety of floral structure is almost equalled by the numerous devices developed by fruit and seed to secure their own dispersal.

While the production of fruit and seed is essentially a sexual process, many seed-forming plants are also capable of being propagated by such vegetative means as bulbs, tubers, cuttings, &c.

The separation of vegetative parts to form new individuals is common in all sections of the plant kingdom. If such parts are cultivated under the same conditions of environment, the method ensures an exact repetition of the individual in all its features, structural and functional. Whilst the procedure has its merits in the retention of desired qualities, it does not, however, offer scope for change; that is, vegetative propagation gives no opportunity for variation.

The seed, on the other hand, is endowed with a wider heritage, for it is a product of the fusion of two specialized cells which are usually of different parentage. The seed, therefore, may not only partake of the characters of two individuals but may also possess others which are different from those of either of the parent stocks.

From the point of view of the study of inheritance in the higher plants the flower is important, for it is the structure which produces these specialized or sexual cells. These cells or **gametes** carry the hereditary factors, and at fertilization they combine to form the embryo-plant within the seed.

Seed production is a periodic phenomenon. Some plants, e.g. Charlock (*Brassica Sinapis*), Groundsel (*Senecio vulgaris*), pass through their life-cycle from seed germination to seed production in one season, while others, e.g. Chickweed (*Stellaria media*), Shepherd's Purse (*Capsella Bursa-pastoris*), may repeat the cycle and remain in flower practically all the year round. All these are called **annuals.** Others, such as the Carrot plant (*Daucus Carota*), Turnip (*Brassica Rapa*), also start from seed, but during the first season of active growth they store food upon which they draw when producing blossom, fruit, and seed in the next growing season. These are **biennials.** But the great majority of herbaceous plants, e.g. Foxglove (*Digitalis purpurea*), Primrose (*Primula vulgaris*), Dandelion (*Taraxacum officinale*), and all shrubs and trees, exist for several years. They are called **perennials** and usually produce flowers and seed every year.

The production of flowers on a plant follows much the same plan as that of ordinary buds on a vegetative shoot. Before we describe the mode of development of floral buds, the mature structure of a simple type of flower, such as that of the Lesser Celandine (*Ranunculus Ficaria*) (fig. 1), or any other species of *Ranunculus*, e.g. Buttercup (fig. 2), will be examined.

The Celandine flower is protected by an envelope which consists usually of three members (the Buttercup has five) which resemble the scale leaves of a vegetative bud. They differ from those of the

Fig. 1. *Ranunculus Ficaria.* The Lesser Celandine.—A, flower bud, B mature flower, C median section, D sepal, E petal with nectary at base, F stamens and mode of dehiscence, G carpel showing horseshoe-shaped stigma, H section of a carpel with a basal anatropous ovule, I receptacle showing scars of the floral members, J compound fruit of achenes of Buttercup (*R. acris*).

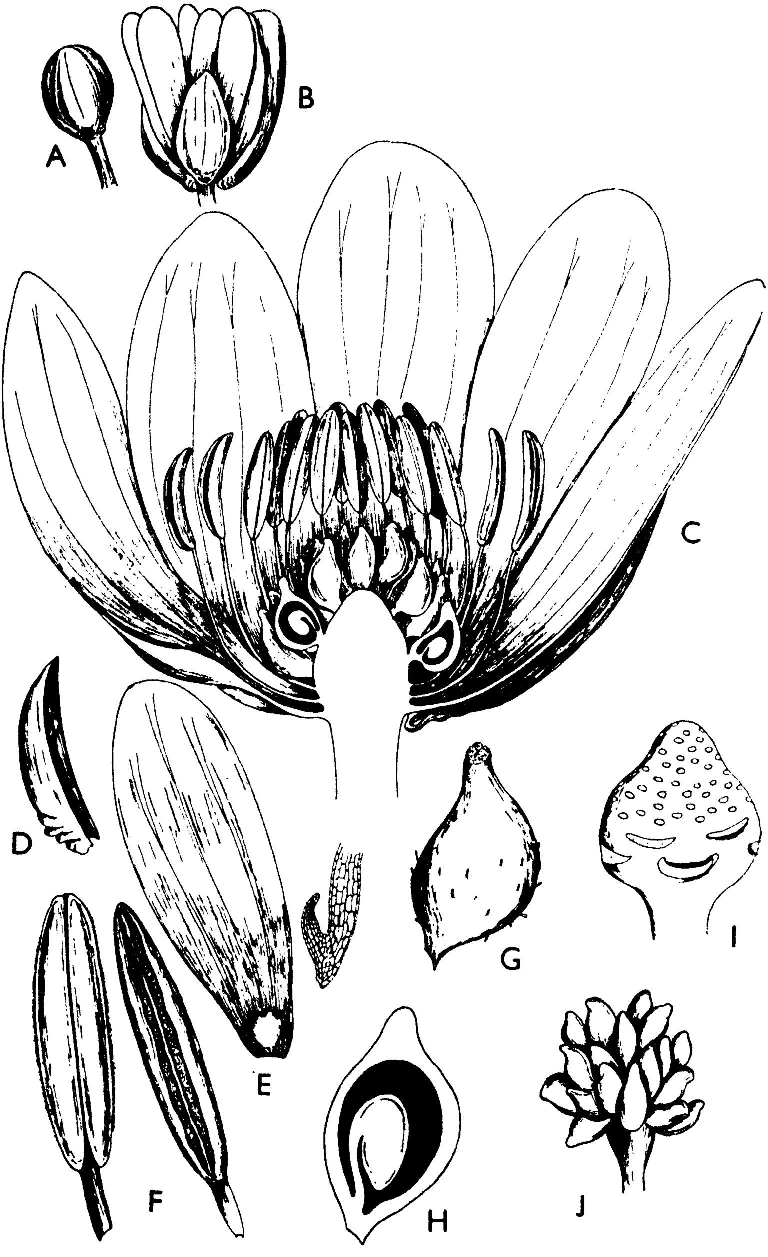

Fig. 1. (For description, see opposite)

ordinary bud, however, in being of softer texture, and appear more like green leaves. These outermost floral leaves are called **sepals** and collectively form the **calyx** of the flower.

When these are removed, yellow floral leaves of softer texture than the sepals appear; these are called **petals** and together constitute the **corolla.** Each petal is veined in much the same way as a leaf, and at the base there is a small scale which forms a pocket wherein nectar is stored. The sepals and petals are inserted separately on the axis in rings or whorls. The coloured corolla is very conspicuous and renders the flower attractive to insects. The calyx and corolla are often referred to together as the **perianth.**

The remaining members, the **stamens** and **carpels,** are arranged on the axis in a continuous spiral.

The **stamens,** collectively referred to as the **andrœcium,** are very numerous in the Celandine and Buttercup, and are very different in appearance from both sepals and petals. Each stamen consists of two parts, a somewhat cylindrical head or **anther** and a slender stalk or **filament.** The anther is divided by shallow longitudinal grooves into four lobes. Each lobe contains a pollen-filled cavity or **pollen-sac** which extends the whole length of the anther. The pollen grains are called **microspores,** and later give rise to the male sexual cells or male gametes. The stamen may therefore be referred to as a spore-bearing leaf or **sporophyll** furnished with four sacs or **microsporangia** containing the pollen or microspores.

Finally, to complete the dissection of the simple Celandine flower, the stamens are succeeded by a number of **carpels,** termed collectively the **pistil** or **gynœcium.** Each carpel is greenish in colour, and consists of a dilated basal region or **ovary** which encloses a single **ovule,** the future seed. The apex of the ovary is continued into a short neck or **style** which expands at the end into a small papillose and adhesive area called the **stigma,** on which may probably be seen a number of pollen grains, possibly conveyed thither by insect visitors. Microscopic examination of the ovule shows that it contains a single spore called the **megaspore** or **embryo-sac.** The carpel enclosing the ovule, as in the case of the stamen holding the pollen, may also be called a **sporophyll,** and the ovule itself (or more correctly the tissue within it surrounding the megaspore) a **megasporangium.**

After removal of all four sets of floral members, the cone-shaped axis or **receptacle** which bore them is strongly reminiscent of the elongated axis of a vegetative bud. Whilst this feature is evident in primitive flowers, such as Celandine and Buttercup, the receptacle varies considerably in other types of floral construction. Whereas the axis of the vegetative bud, by virtue of apical growth, is capable of elongation with continued production of leaves, the floral bud is essen-

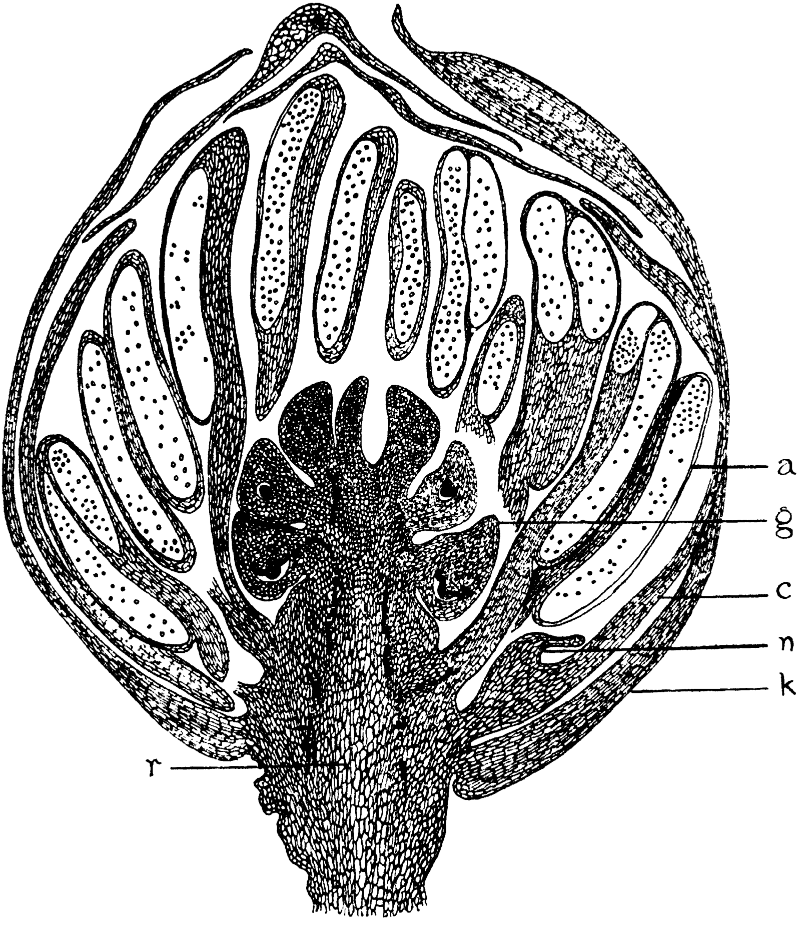

Fig. 2. *Ranunculus acris.* The Buttercup.—Median section. *r* cone-shaped receptacle, *k* calyx, *c* corolla with a nectary scale *n*, *a* andrœcium, *g* gynœcium with young ovules in some of the carpels.

tially a structure of limited growth, for with the formation of carpels its development is usually complete. The receptacle is, therefore, an abbreviated axis, and whilst the vegetative shoot, having an apical meristem, may also be furnished with axillary buds, no buds are found (except in rare instances) in the axils of the floral members.

A flower may now be defined as a shoot of limited growth, having a short axis or receptacle bearing four sets of floral members, namely, sepals, petals, stamens, and carpels. A study of the floral types in Part II of this book will, however, show many exceptions to this broad definition of a flower.

The comparison of a flower with a leafy shoot does not imply that the parts of the flower have been derived from foliage leaves by modification. It is true that the sepals resemble foliage leaves, but in the case of the petals, and of the stamens and carpels in particular, there is not much similarity. All the evidence in relation to the evolutionary history of sporophylls in general, including plants of lower grade than the Angiosperms, points convincingly to the fact that they have not been derived from foliage leaves. It will, however, often be convenient when elucidating their mode of development to refer to the floral members as leaf-like organs, but as long as it is borne in mind that they are specialized structures, their comparison with foliage leaves need not be further considered.

Although two very distinctive groups of Angiosperms are recognized, **Dicotyledons** and **Monocotyledons,** they agree closely in fundamental features of floral development. They differ, however, not only in the number of **cotyledons** ("seed-leaves"), which, with few exceptions, is **two** in the former and **one** in the latter, but also in vegetative features, the shape and venation of the leaves, internal structure of the stem, number of floral members and mode of formation of the **embryo** or young plant in the seed (pp. 94, 147, 149).

CHAPTER II

Inflorescences

Flowers are rendered conspicuous by virtue of their size and colour. It has been established by actual experiment that insects of various kinds, chiefly bees, are attracted to flowers by virtue of mass-colour or scent, or both. Such insect visitors, activated presumably by their desire to get food from the flower in the form of pollen or nectar, incidentally perform the important work of pollination, which is a necessary preliminary to fertilization and production of seed. Flowers which are pollinated through the agency of wind are neither scented nor attractively coloured.

Many devices exist whereby the flowers on a plant are made conspicuous, not only by their being massed together if they are small, but by their being arranged in diverse ways on tall and frequently branching stems.

The mode of arrangement of flowers on the individual plant is known as its **inflorescence.** Inflorescences are of various kinds, and each type is usually constant for the species. The production of a single flower on the individual plant, e.g. Tulip, when the inflorescence is said to be **solitary,** is somewhat rare, and most plants make a good display of their flowers in point of number.

Inflorescences are grouped into two classes, **Indefinite** (or Racemose) and **Definite** (or Cymose) (fig. 5).

A type of an indefinite inflorescence may be illustrated by either the Lupin (*Lupinus polyphyllus*) (figs. 3, 49) or the Foxglove (*Digitalis purpurea*) (fig. 58). In both these types the flowering axis (or **peduncle**) bears the oldest flowers at the base and the youngest at the top. Each flower arises in the axil of a reduced leaf or **bract.** Bracts appear along the peduncle in the same way as do the ordinary foliage leaves on the vegetative stem, and accordingly towards the apex they decrease in size; in their axils they protect the young flowers of the inflorescence. In the Lupin the bracts fall off as the flowers open, but in most plants, as in the Foxglove, they remain, while in other inflorescences they may be greatly reduced or even be entirely absent, as in the Wallflower (*Cheiranthus Cheiri*) (fig. 41, A). In the Lupin or Foxglove type of inflorescence, therefore, the flowers may be fully mature at the

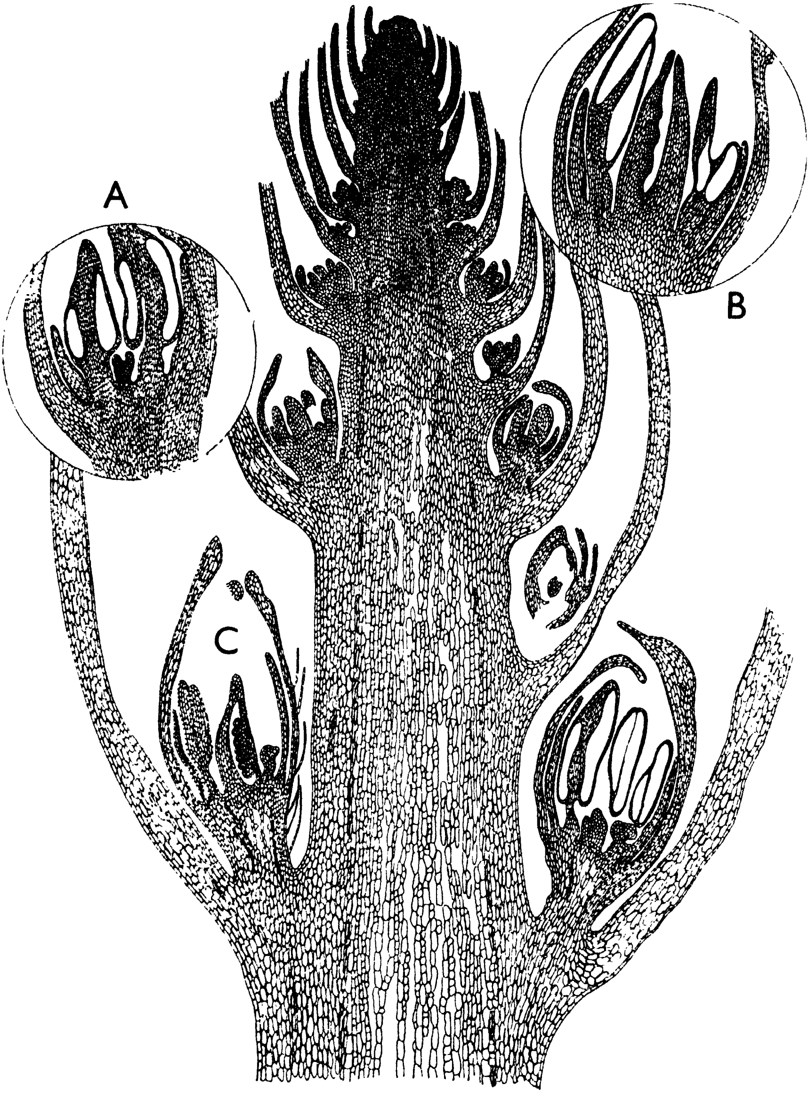

Fig. 3. *Lupinus polyphyllus.* The Lupin.—Median section of the inflorescence apex. The apical meristem is devoted entirely to the formation of flowers arising singly in the axils of the bracts. A, early stage in formation of single carpel, as a stalked cup split open facing the posterior axis. B later stage showing elongation of tubular carpel, still open at the top; beginning of ovule formation indicated by slight protuberances within. C carpel completely closed at the top by the style; later stage in ovule formation.

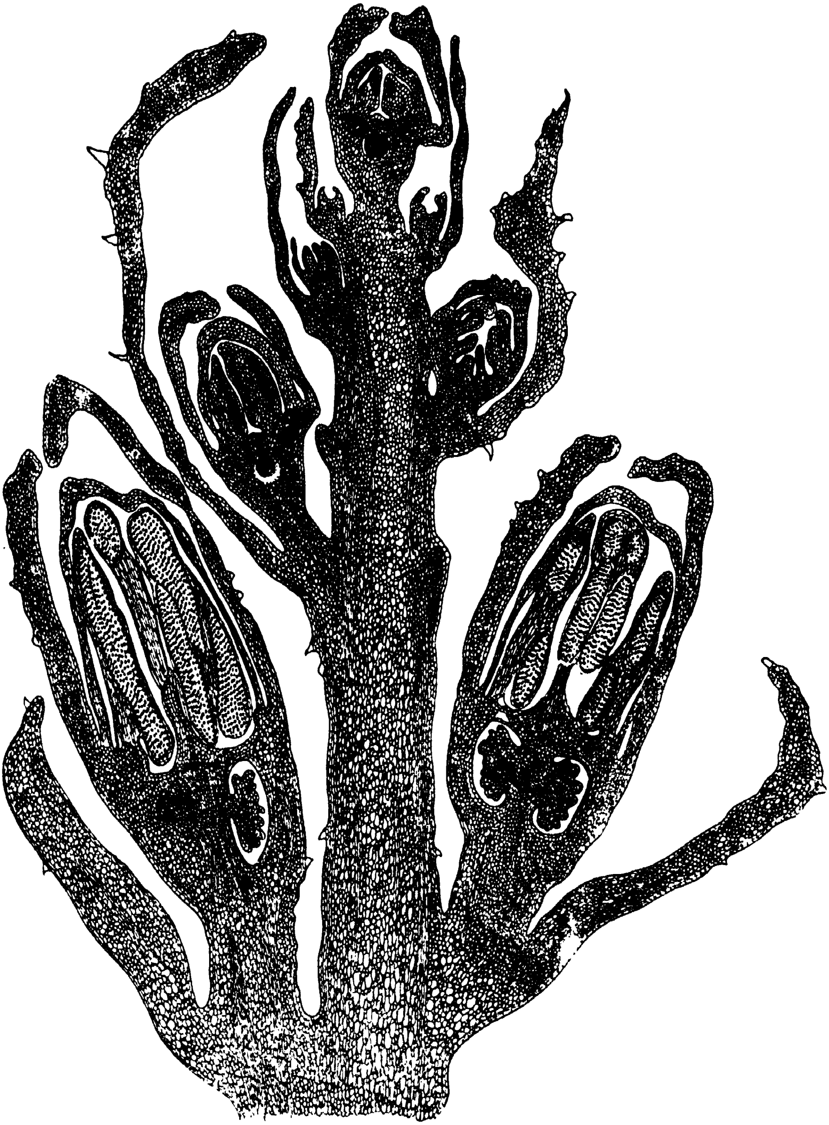

Fig. 4. *Campanula persicifolia.*—Longitudinal section of young inflorescence-bud showing racemose and cymose development; in addition to bearing a number of axillary flowers the axis terminates in a flower.

base of the axis while those near the top are still unopened. Although this manner of " indefinite " or continuous production of flowers from the growing point of an axis is common to a wide range of plants, there are various and specific ways in which the flowers are grouped together on the common axis.

If the flowers of an indefinite inflorescence are furnished with stalks (**pedicels**) as in Lupin and Foxglove, the type is called a **raceme** (fig. 5, A). When the oldest flowers are raised to the level of the youngest owing to their having longer stalks, as in the Wallflower, the form is called a **corymb** (fig. 5, B). An indefinite type of inflorescence in which the flowers are arranged as in the raceme but without stalks, as in the Spotted Orchis (*Orchis maculata*), is termed a **spike** (fig. 5, C). In another form known as an **umbel** (fig. 5, D) all the flowers and bracts appear to arise from the end of the axis, but the oldest flowers still lie towards the outside and the youngest near the apex of the axis. The whorl of bracts surrounding the umbel is known as the **involucre.** Umbel inflorescences, as in the Carrot plant (*Daucus Carota*), Cow-parsnip (*Heracleum Sphondylium*), Beaked Parsley (*Anthriscus sylvestris*) (fig. 54, A), &c., are a characteristic feature of the family *Umbelliferæ.* In some types of this family the involucre is absent or only partially represented, when it is described as an **involucel.** Finally, if an umbel type is condensed by the elimination of its flower stalks, the apex of the growing axis must expand like a knob or saucer in order to accommodate the developing flowers; the growing point, as in the umbel, is still at the centre of the expanded axis and is surrounded by the sessile flowers, the youngest near the middle and the oldest towards the margin. This type (fig. 5, E), found in the Daisy (*Bellis perennis*) (fig. 61, A), the Dandelion (*Taraxacum officinale*) (fig. 60), &c., is called a **capitulum,** and is characteristic of the Dandelion family, the *Compositæ.* Like the umbel, the capitulum is invested with a prominent involucre of bracts. In some members of the family, e.g. Sunflower (*Helianthus annuus*) (figs. 10 and 22), the small flowers arise in the axils of minute bracts called interfloral bracts, but in general, as in the Dandelion (fig. 60, A), these internal bracts of the inflorescence are absent. The flowers of a capitulum are so small (hence they are called "florets") and so closely crowded together on the flattened axis that the whole inflorescence, e.g. of a Dandelion, is often erroneously called a single " flower ".

The above types of indefinite or racemose inflorescences agree in that all their flowers develop in succession from a common growing point at the apex of the axis. Compound inflorescences of this class are common. They are called compound racemes, umbels, spikes, &c., when, in place of single flowers in the axils of the bracts, there arise branches or secondary axes which are themselves racemes, umbels,

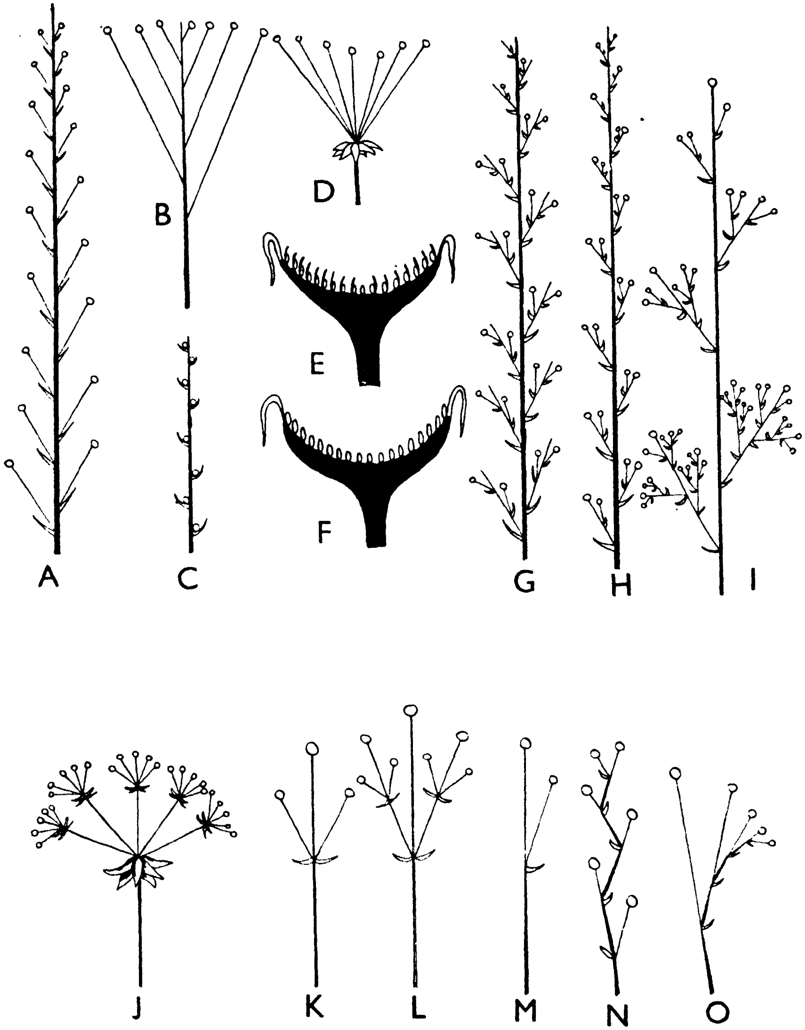

Fig. 5. *Types of Inflorescences.*—A raceme, B corymb, C spike, D simple umbel, E capitulum with interfloral bracts, F capitulum without interfloral bracts, G compound raceme, H mixed; main axis racemose with axillary cymes, I panicle, J compound umbel, K and L dichasia, M monochasium, N scorpioid cyme, O helicoid cyme.

&c. The term **panicle** is somewhat loosely applied to these compound forms, especially if the basic plan is that of the simple raceme; it is also applicable to compound cymose types (fig. 5, I).

The **definite** or **cymose** class of inflorescence is also a well-defined system of floral arrangement. The fundamental difference between the two classes is that in the development of the definite type, the growing point of the axis, sooner or later, becomes used up in the formation of a *terminal* flower. Before this actually takes place the growing point may form a number of floral buds in the same way as described above for the racemose inflorescence (fig. 3), but when the apex forms a terminal flower, no further extension of the axis is possible (fig. 4). Hence the term " definite " for this system, which ultimately entails a check to the forward growth of its axis. Further extension of a definite inflorescence, however, may be provided if one or more sub-terminal buds produces either a single flower or a secondary axis which may develop into a branch inflorescence.

A simple type of a definite inflorescence is shown by the Bladder Campion (*Silene inflata*) (fig. 45) or the Stitchwort (*Stellaria Holostea*) (fig. 43). Here, the growing point forms a terminal flower, but in the axil of each of the two opposite leaves (which thus function as bracts) a little below this flower, a branch arises which also terminates in a flower. On each of these axes again two opposite bracts with flowers arise, the whole system resulting in a symmetrical inflorescence known as a **dichasium** (fig. 5, K and L). The dichasial type may be extended further by a regular formation, in one plane, either of pairs of flowers or of additional floral axes. Dichasia appear complicated (e.g. *Gypsophila*) if the system of paired branching is repeated in several planes around the parent axis.

A second type of definite inflorescence is known as a **monochasium.** This type also shows the usual formation of a terminal flower, but further extension of the inflorescence is carried on by a single sub-terminal bud which arises in the axil of a bract. One type, known as a **helicoid** monochasium (fig. 5, O), shows all the flowers in a downward curve to one side of the parent axis. This arrangement is brought about by the second flower arising on the axis of the first, the third flower on the axis of the second, and so on, and during their formation the whole system curls over towards the first axis. Another monochasial type, known as a **scorpioid** cyme, starts in the same way by forming a terminal flower, but its axis bends over to one side, say the right, and when the sub-terminal bud on this axis produces the second flower, the axis of the latter bends over to the left, and successively formed axes with their flowers bend over alternately right or left (fig. 5, N). This type of growth exhibited by monochasial inflorescences, whereby continuation is effected by successive lateral buds, is known as sympodial, and the term **sympodium** may be applied to either of the types specified above.

It is not always easy to determine the exact nature of an inflorescence when it is of a **mixed** type, partly indefinite and partly definite. Thus, that of the Figwort (*Scrophularia nodosa*) (figs. 5, H, and 59, A) shows a main axis which is " indefinite " (no terminal flower), but the secondary axes arising in the axils of the opposite leaves are " definite " (terminating in a flower).

The foregoing is an outline of the general structure of inflorescences; special cases are described in connexion with the floral types in which they occur. (See Part II.)

CHAPTER III

Development of the Flower

We have seen that inflorescences follow well-defined laws of development. Closer examination of the way in which the individual flowers are inserted on the inflorescence axis shows that they also have a fixed orientation in relation to this axis and to the bract associated with them (fig. 6).

The normal position (the terminal flower being ignored for the moment) of the flower is in the axil of the bract. The bract is thus "in front" of, and the axis "behind", the flower. Accordingly, that half of the flower which faces the bract is called the **anterior** part, and the other half which faces the inflorescence axis the **posterior** part; and a plane cutting vertically through the middle of the bract and the axis would therefore divide the flower, in half, in the **median** or **antero-posterior** plane. Again, a vertical section through the middle of the flower but at right angles to the median plane would cut the flower in the **lateral** plane.

A typical flower has been described above as consisting of four sets of floral members, namely, sepals, petals, stamens, and carpels,

Fig. 6. *Actinomorphy and Zygomorphy: Principles of the floral diagram.*

A to D, *Actinomorphy.*—A, position of a typical flower in relation to the subtending bract, which is *anterior*, and to the inflorescence axis, which is *posterior*. Note the two laterally placed prophylls on the pedicel of the flower. B front view of flower, the bract at the base, and the axis behind the flower; the "top" petal is posterior and the sepal and stamen at the "base" are anterior. A plane cutting the diagram at right angles to the paper and passing through the centre of the axis and the middle of the bract is the antero-posterior plane, which therefore bisects the flower as shown in C, the median section of flower; the figure shows the right-hand half of B, showing the anterior sepal and stamen cut through, and on the left is the cut posterior petal; the other two petals are intact; two stamens are shown behind the ovary which on the right has been cut through a partition and on the left through a loculus. D conventional floral diagram; compare with B. The small crossed-circle stands for the posterior axis, and at the bottom is the anterior bract; note also the alternate positions of all the floral members in the successive whorls; the two small prophylls are in the lateral plane. Floral formula $K_5C_5A_5G_{\underline{(5)}}$.

E to H, *Zygomorphy.*—E side view of a typical zygomorphic flower; posterior axis on right and anterior bract on left; the vertical hood is posterior ("back" to the axis) and the lower "lip" is anterior (facing the bract). F front view; the posterior hood consists of two petals, the two smaller lobes are lateral petals, and the anterior lobe or lip represents one petal. G median section; note posterior hood and anterior lip. H floral diagram with axis and bract in position. Floral formula $K_{(5)}[C_{(5)}A_{2+2}]G_{\underline{(2)}}$.

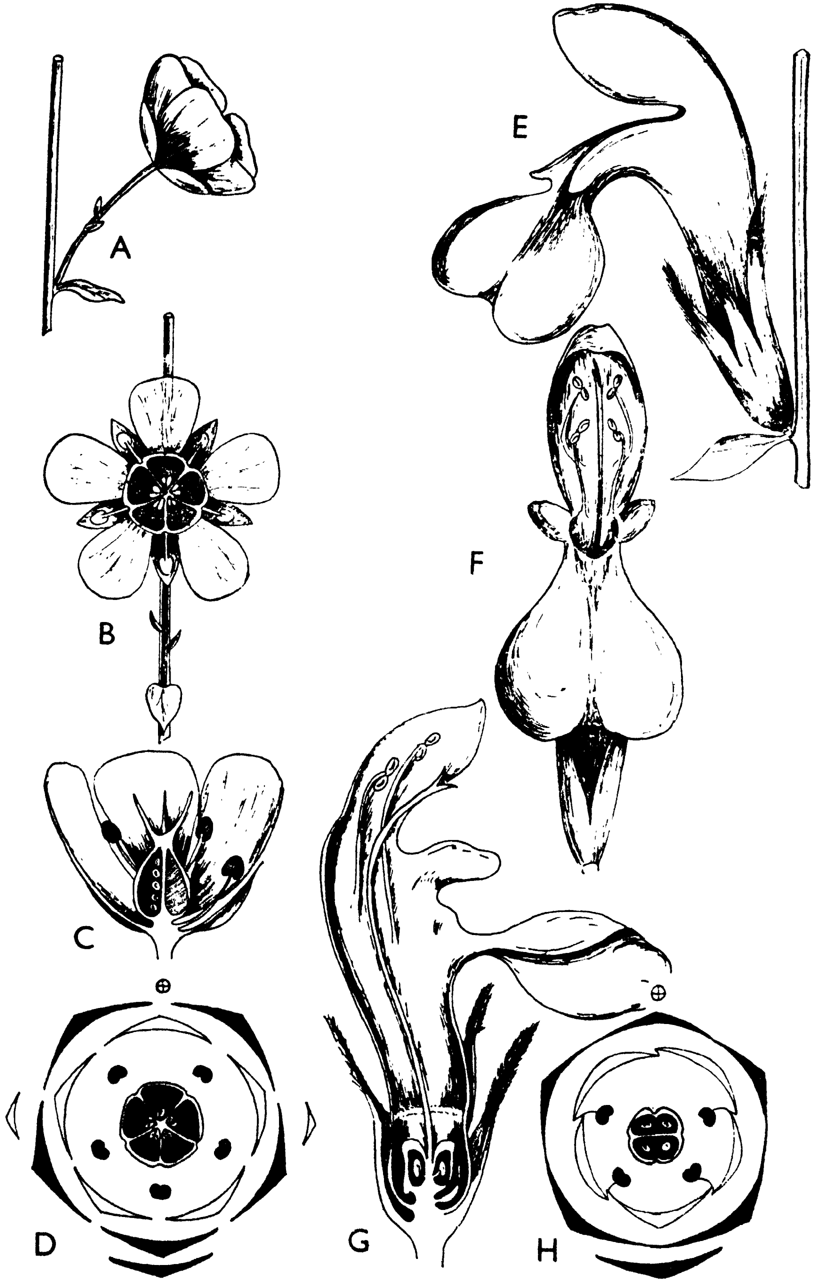

Fig. 6. (For description, see opposite)

all borne on a receptacle which is continued below into a flower-stalk or **pedicel.** On the latter, at a little distance below the flower, there are frequently found small bracts, called **bracteoles** or **prophylls.** In the flowers of monocotyledonous plants the bracteole is single and is inserted on the pedicel posteriorly, that is, facing the axis, but in dicotyledonous plants there are two bracteoles, one on each side of the pedicel, in the lateral plane.

The mode of development of the Buttercup (fig. 7) illustrates a simple type of floral construction. In the same manner as a vegetative bud arises in the axil of a foliage leaf, the floral bud begins its growth as a smooth cone-shaped mass of tissue in the axil of a bract. The first organs to appear are at the base of this meristematic cone, and they are the two bracteoles, one on each side in the lateral plane. They are soon followed, a little way above, by the rudiments of the five sepals, which are seen as small lumps or primordia of tissue at the same level and equally spaced from one another; that is, they form a ring or whorl. The young sepals grow quickly, soon over-topping the bracteoles, for they perform the function of protecting the later-formed parts of the flower bud.

Succeeding the sepals, at a slightly higher level on the cone of tissue which may now be called the receptacle, and at points alternating with them, there arise an equal number of lumps or primordia which become petals. Petal development is relatively slow in comparison with that of the remaining members of the flower, the stamens and the carpels.

If a close spiral is now described around the remainder of the cone-shaped receptacle, starting immediately above the whorl of petal-primordia and culminating at the apex, the stamens, followed by the carpels, originate on it as numerous primordia. They arise in close succession along the spiral, about three-fourths of the spiral being devoted to stamens and the rest to carpels.

Fig. 7. *Development of the flower.* Diagrammatic.—A, side view of floral bud standing between bract (left) and axis (right), showing one of the lateral prophylls. B later stage, front view, bract pulled down to show the two prophylls and the primordia of the sepals. C rapid growth of sepals to protect bud. D equal growth of sepal primordia. E unequal growth of sepals, side view. F zonal growth below petal primordia forming corolla tube (sympetaly), the petal lobes being equal (actinomorphy). G zonal growth as in F, but petal primordia of unequal growth (zygomorphy). (Cf. fig. 6, G.) H bud showing primordia of all the floral members, prophylls at base, sepals above succeeded by petals and alternating with them, followed by numerous primordia of stamens and finally at the apex by horseshoe-shaped carpellary elements, all borne on the ovoid or cone-shaped receptacle. I receptacle showing staminal primordia well advanced but the carpellary primordia still relatively small. J bilobed stamen with lateral grooves. K the same cut across, showing four-lobed contour and four pollen sacs. L the same in section, showing pollen sacs, connective and vascular bundle. M zonal growth, forming staminal tube below stamens of a leguminous flower.

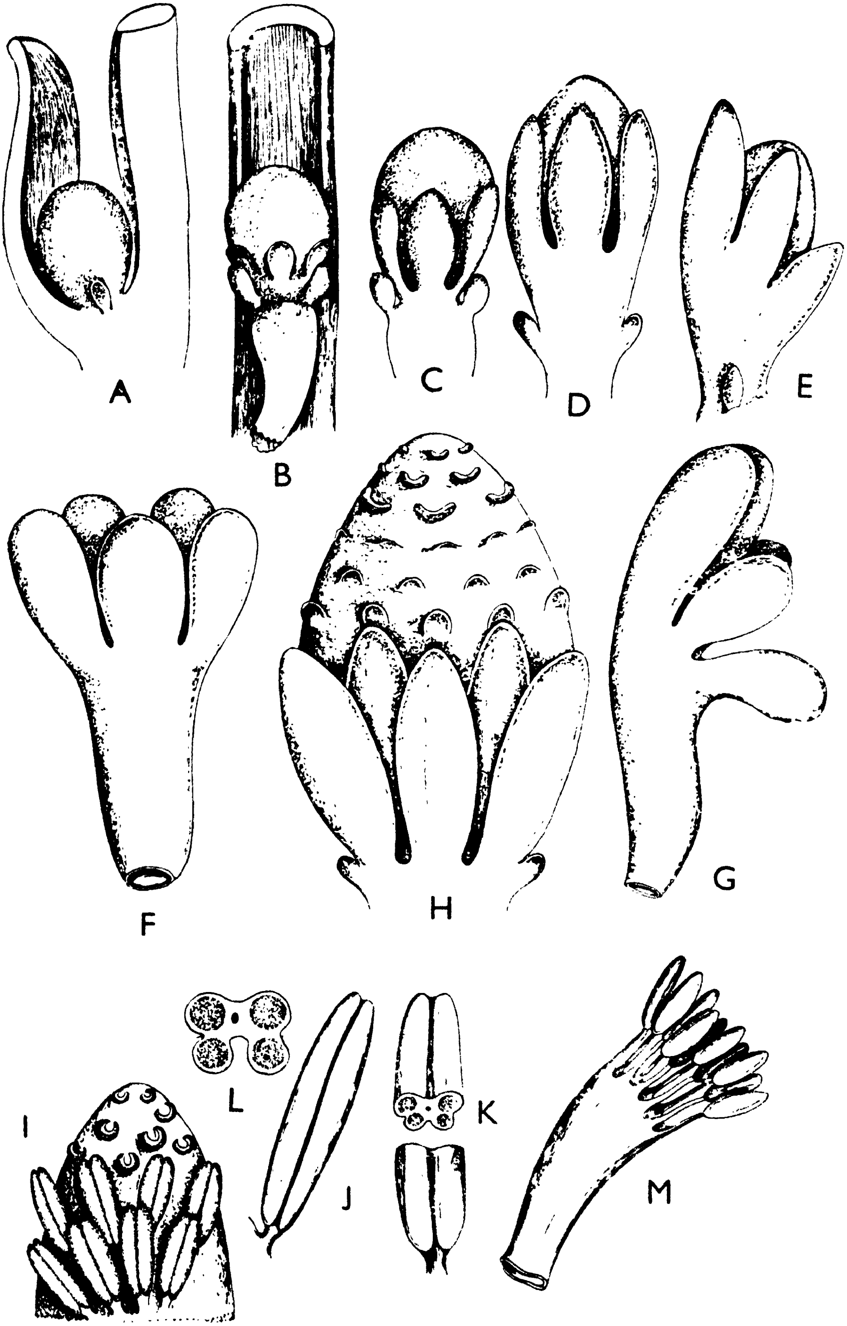

Fig. 7. (For description, see opposite)

When all the floral members are organized, the cone-shaped meristem ceases to grow and constitutes, as mentioned, the receptacle of the flower.

Just as a vegetative bud bursts its enveloping scales by growth and expansion of its axis and young leaves, so also the opening of the flower bud is effected by the rapid development of its retarded corolla, assisted by the projection of the stamens as a result of the elongation of their filaments, and by a general expansion of the receptacular axis.

The above brief description is characteristic of primitive types, such as those of the Buttercup family, in which all the floral members are free from one another. The floral envelopes, the calyx and corolla, are laid down in whorls, and the stamens and carpels in a continuous spiral. In still more primitive types of this family, e.g. the Marsh Marigold (*Caltha palustris*), all the floral members are spirally arranged on the receptacle. The great majority of flowers, however, observe a whorled arrangement throughout. In more advanced types of flower the primitive cone-shaped receptacle tends to become more and more flattened. In higher types again, the growing point of the receptacle is depressed, so that the receptacle becomes concave or even cup-shaped, and in those types of floral construction exhibiting high evolutionary status, the carpels are actually enclosed within a deep hollow receptacle.

We have seen that the members of all four sets of floral organs originate on the receptacle in much the same way, as protuberances of tissue called primordia. The main features of floral development which involve fusions and modifications of the primordia in more advanced types will now be described.

(*a*) The Calyx

When the primordia of the sepals remain independent of one another during their whole development, as in the Buttercup, the calyx is said to be free or **polysepalous.** Frequently, however, after a certain amount of independence the primordia are raised up on a common zone of growth at their bases. This zone projects as a short tube on which the young sepals appear as a number of teeth or lobes. Hence arises the condition of a tubular calyx, or **gamosepaly** (joined sepals) as in the Primrose (*Primula vulgaris*) (fig. 55, I), the Bladder Campion (*Silene inflata*) (fig. 45, B), &c., as opposed to **polysepaly** in the Buttercup. In the *Caryophyllaceæ* (p. 172), this feature of the calyx is responsible for the subdivision of this family into two groups, namely, *Alsineæ* (sepals free), as in the Stitchwort (*Stellaria Holostea*) (fig. 43), and *Sileneæ* (sepals joined), as in the Bladder Campion (fig. 45, B).

In some cases the sepal primordia do not grow forward at the same rate, and when inequality of growth extends into the calyx tube as well the tubular calyx becomes irregular in shape. Thus in some members of the *Leguminosæ* family, e.g. the Gorse or Whin (*Ulex europæus*) (fig. 48), and the Common Broom (*Sarothamnus scoparius*) (fig. 47), the five sepal primordia remain distinct only for a very brief period, after which, by zonal growth, they are raised up on a short wide tube which again grows more on its posterior side than on its anterior side. This differential development results in a bilobed condition of the calyx, but three minute teeth on the lower (anterior) lobe and two on the upper (posterior) lobe give the clue to the number of sepals in these flowers.

A number of flowers of the Buttercup family, the *Ranunculaceæ*, require special mention on account of their sepals being attractively coloured, thus resembling petals (petaloid). In the Globeflower (*Trollius europæus*) (fig. 39, A), Christmas Rose (*Helleborus niger*), Monkshood (*Aconitum Napellus*) (fig. 40), &c., the true petals are so reduced or modified and entirely hidden by the sepals that the function of the corolla is undertaken by the coloured calyx, which is the most prominent part of these flowers. There are, however, some types of this family which do not possess a corolla at all, and the floral envelope constituting the calyx is again coloured like a corolla, e.g. the Wood Anemone (*Anemone nemorosa*) (fig. 38, A), Clematis or Traveller's Joy (*Clematis Vitalba*) (fig. 38, F), and Marsh Marigold (*Caltha palustris*) (fig. 39).

The family *Ranunculaceæ* thus includes a series of types, some of which, like the Buttercup, possess in the calyx and corolla two distinctive floral envelopes; in others, as in the Monkshood, where the petals are reduced, the function of the corolla is taken over by the calyx, which becomes petaloid; in others, again, as in the Marsh Marigold, the single floral envelope discharges the functions of both calyx and corolla.

It is interesting to note that in those types of the *Ranunculaceæ* which show reduced petals, the latter are represented by curious structures which in appearance are somewhat intermediate between petals and stamens (see Globeflower, fig. 39, C). In the evolutionary history of the floral members, there is reason to believe that the petals may have been derived by modification from some of the outermost members of the andrœcium. Some of the above-named types which are in possession of only one floral envelope, the calyx, are therefore deemed to be more primitive than those in which the double envelope of calyx and corolla is present.

A somewhat extreme modification of the calyx is shown by several members of the *Compositæ* family; in the Dandelion (*Taraxacum officinale*) (fig. 60, C), Coltsfoot (*Tussilago Farfara*) (fig. 60, I), &c., it takes the form of numerous silky hairs (the " pappus ") which help in fruit dispersal. In many types of this family, again, e.g. the Daisy (*Bellis perennis*) (fig. 61, C), the calyx is absent, and in others, e.g. the Sunflower (*Helianthus annuus*) (fig. 10), it is reduced to mere scales. In the *Umbelliferæ* family the calyx is frequently absent or represented by a narrow ridge above the ovary. In these two families, in which the individual flowers are very small, the protective function of a calyx appears to be taken over by the involucral bracts of the inflorescence.

(*b*) The Corolla

In the simpler types of flower the petal primordia remain distinct from one another during their whole development, so that a condition of free petals or **polypetaly** is maintained. In the more advanced types, however, the petal primordia, after a more or less brief period of separateness, are raised up in the manner described above for the gamosepalous calyx. In the case of the corolla, the zonal or intercalary growth below the primordia often becomes very prominent, and the tubular part so formed frequently becomes the most conspicuous feature of the corolla, namely the corolla-tube, as in the Foxglove (*Digitalis purpurea*) (fig. 58), &c. In certain flowers thus furnished with tubular corollas, intercalary growth begins so early that it is often difficult to determine the number of petals in the corolla. Examination of the open end of the tube, however, often reveals a lobed condition, the number of lobes being an indication of the number of original petal primordia. Thus in the Foxglove the corolla is almost completely tubular, but the mouth of the tube shows from its lobed condition that five petals are present.

A corolla in which the petals are thus united, however slight the union at the base may be, is said to be **sympetalous** (or gamopetalous).

Fig. 8. Development of *Hypogyny* in *Myosotis sylvatica*, Wood Forget-me-not.—Median section of the flower-bud showing insertion of the calyx *k* and corolla *c*, immediately below the ovary. The scales *sc* partly close the mouth of the corolla. The stages A to I in the development of the flower were obtained from the same young inflorescence. A, youngest stage of the flower as an undifferentiated protuberance; B later stage; C beginning of calyx (*k*) and corolla (*c*) primordia; D appearance of the anthers *a*; E anthers inserted on the corolla (epipetaly) by zonal growth below the latter; note appearance of carpel promordia *g*; F epipetalous anther *a* showing formation of sporogenous tissue; note advance of carpels; G carpels closing in and ovules appearing at base of ovary; H apical growth of individual styles and further differentiation of ovules; I gynœcium completely closed in over the ovules, which are in basal placentation; J nearly mature bud with stylar column almost completely filled with tissue.

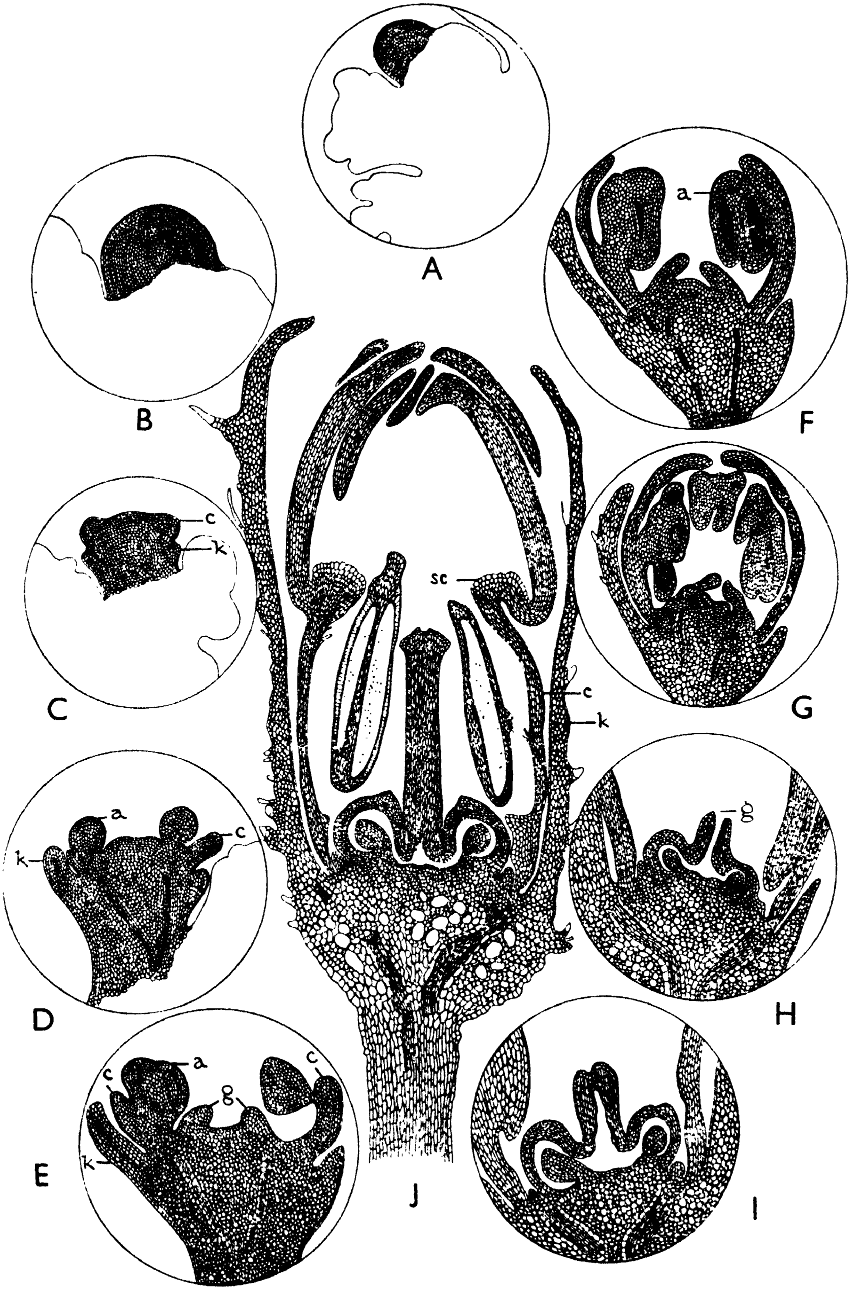

Fig. 8. (For description, see opposite)

The presence of sympetaly is not always evident; thus in the Primrose (*Primula vulgaris*) (fig. 55), the joined petals are so deeply notched as to appear free from each other, and in the Speedwell (*Veronica Chamædrys*) (fig. 59, G) this apparent polypetaly is much more pronounced, but in both these types the corolla can be detached in one piece.

When the petal primordia and the corolla tube, if present, grow forward at the same rate, the corolla is said to be **regular** or **actinomorphic** (fig. 7, F). If the primordia develop at an uneven rate, yielding petals of unequal size and shape, the corolla is described as **irregular** or **zygomorphic** (fig. 7, G). This feature of unequal development in a sympetalous corolla may affect not only the size of its lobes but the shape of the corolla tube as well. This occurs if the zonal growth is more active at some parts than others. It is almost always the rule that the more active primordial growth, resulting in zygomorphy, occurs either in the posterior or the anterior parts of the young flower or in both these. It is in this way that zygomorphic flowers come to possess such prominent features as "hoods", "flags", "spurs", "platforms", &c., as parts of the corolla. Unequal growth of the corolla leading to various degrees of zygomorphy is an important advance in floral evolution and appears to be correlated with insect visitation, involving greater precision in effecting pollination.

The flowers of monocotyledonous plants, in general, unlike those of dicotyledons, possess a perianth (p. 6) in which there is no distinction between calyx and corolla. The flowers in some of the monocotyledonous families (which include the Sedges, Grasses, and Rushes) are of very simple construction; in them a perianth is entirely wanting or represented by rudimentary structures of the nature of scales. It is noteworthy that all these unattractive flowers are pollinated through the agency of wind.

In the higher families of monocotyledons, however, the perianth is highly developed and brilliantly coloured, e.g. Lily, Hyacinth, Daffodil, Iris, Orchis. All these flowers are pollinated by insects.

The perianth of the monocotyledonous flower develops along the lines described above for the floral envelopes of the dicotyledon. It arises in two whorls of three members each; these members are called perianth segments or lobes. Fusion of the segments by intercalary growth, described as **gamophylly,** and the development of zygomorphy, take place in precisely the same way as in the flower of the dicotyledon.

Fig. 9. Development of *Perigyny* in *Prunus Lauro-cerasus*, the Cherry Laurel.—Median section of flower bud showing cup-shaped receptacle *r*, with calyx *k*, and folded petals of corolla *c*. In the bud the anthers *a* are protected within the receptacular cup *r*, the filaments being short and undeveloped; *g*, the unilocular ovary shows two anatropous ovules in pendulous placentation. Inset: (left) the filament *f* of an incurved stamen; (right) at the centre among the anthers is the tip of the style *sl.*

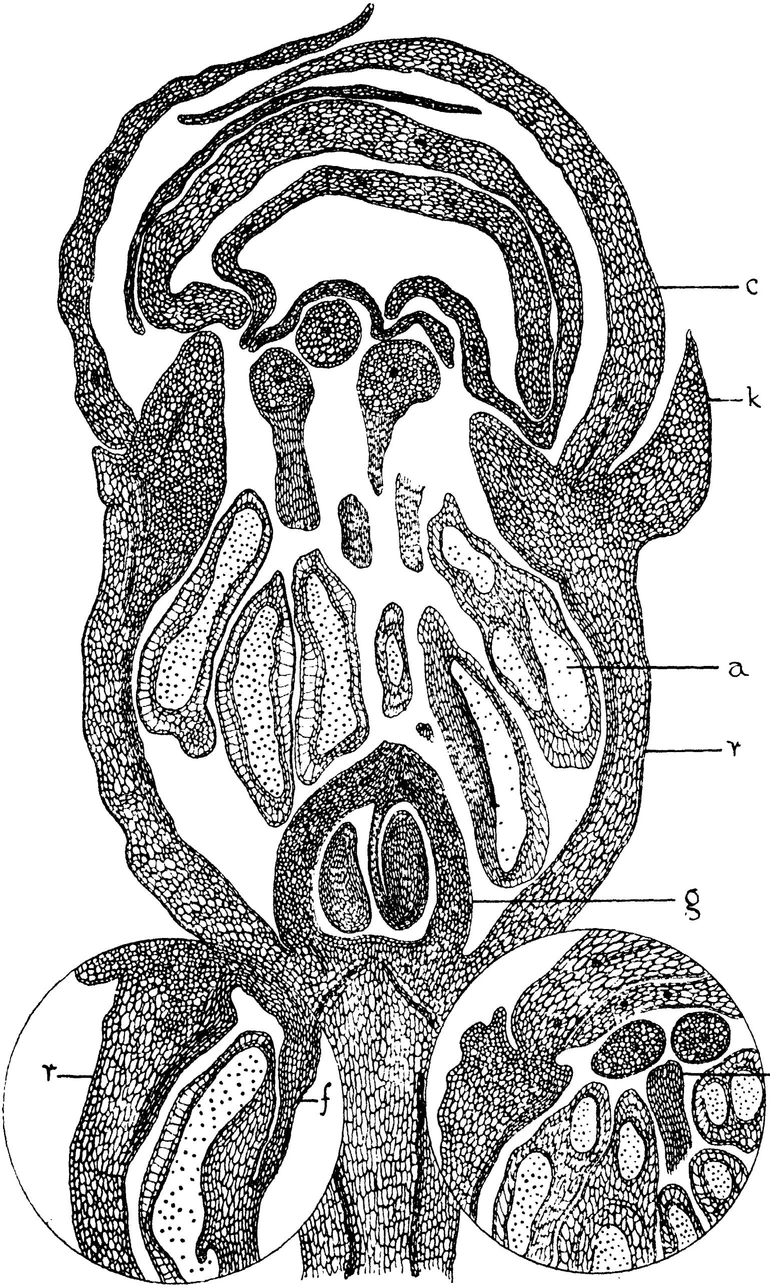

Fig. 9. (For description, see opposite)

(*c*) The Andrœcium

While it is not difficult to recognize a leafy form in sepals and petals, stamens are very different in appearance from foliage leaves, yet in their early stages of development from the primordia they, too, follow much the same lines as ordinary leaves. Instead, however, of the primordia becoming gradually flattened out as they do when forming sepals and petals, their original cylindrical shape is more or less preserved in the mature anther (fig. 7, I, J). Like the lamina of the leaf, again, the anther is the first part of the stamen to develop; the filament, like the petiole of the leaf, is a much later production.

The various stages of development that take place within the anther, culminating in pollen production, are of great importance; they lead to the reproductive phase in flower development and are described in Chap. V. While sepals and petals are only accessory or " non-essential " structures, stamens and carpels are of fundamental importance in sexual reproduction and seed formation; for this reason they are called the " essential organs " of the flower.

In the simple Buttercup type, the staminal primordia arise in large numbers in spiral fashion on the cone-shaped receptacle. The most common formation of the stamens on the receptacle is, however, in one or more rings or whorls; each whorl usually contains four, five, or ten stamens in the flowers of dicotyledonous plants, and three or six in those of monocotyledons.

Flowers like those of the Buttercup family (*Ranunculaceæ*) in which all the floral members are free and there is a multiplicity of stamens (and frequently of carpels as well) are deemed to be primitive forms, whereas in the more highly evolved and complex forms the number of stamens tends to be reduced. A study of these advanced types shows that this economy is usually compensated by the development of certain devices in floral construction which ensure greater precision in pollination by insects.

Fig. 10. Development of *Epigyny* in *Helianthus annuus*, the Sunflower.—A, portion of radial section of young capitulum; the whole development of the flower can be traced in series from the young central florets to the maturer florets towards the margin; note the interfloral bracts *br*; B young flower protuberance; C the primordia of the corolla *c*, appearing before those of the calyx. D the next primordia, those of the stamens *a*. E and F further stages of corolla and anthers; note increasing concavity of receptacle with the primordia of the two carpels *g*. G corolla *c* and anthers *a* raised by a common zonal growth *z*, resulting in epipetaly; note the upward growth of the two carpel primordia. H the same showing the single ovule in basal placentation. I receptacle closed over the unilocular ovary with ovule at base. J young floret complete; note greatly reduced calyx *k* and nectary ring around the base of the style. K transverse section of a floret at the stage indicated in J; note anterior bract, tubular corolla, five anthers, and two joined carpels (cf. fig. 21).

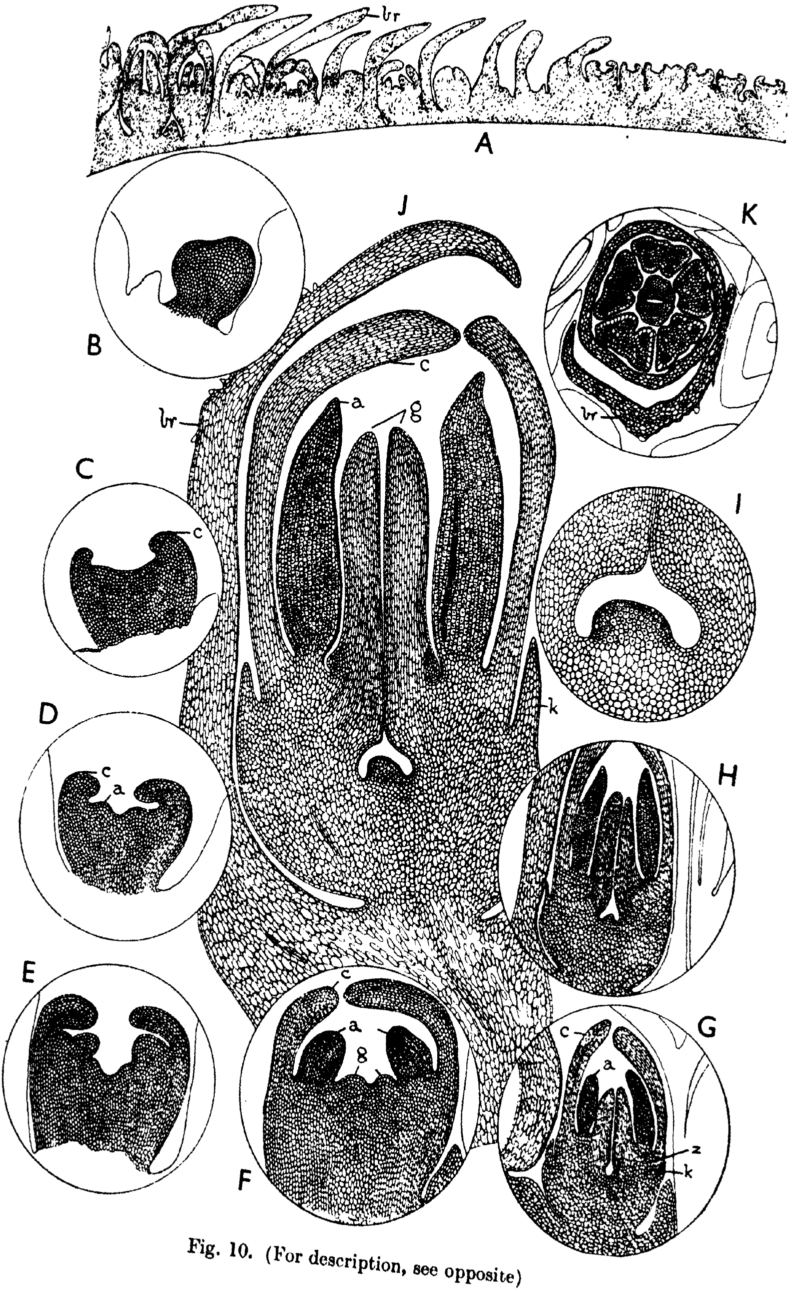

Fig. 10. (For description, see opposite)

The stamen, as stated, arises as a cylinder of tissue on the receptacle. The cylinder is devoted almost entirely to the formation of the anther, and the pollen is often mature long before the stalk or filament at the base of the anther appears.

Zonal or intercalary growth (p. 20) occurs only rarely between the members of the andrœcium. It takes place, however, in many types of the Pea family, the *Leguminosæ*, e.g. Broom (*Sarothamnus scoparius*) (fig. 47), Gorse or Whin (*Ulex europæus*) (fig. 48), Pea (*Pisum sativum*). In these types, after the anthers and their filaments are formed, the stamens are thrust forward by a tubular extension below the bases of the filaments, thus forming a staminal tube (fig. 7, M). In many plants of this family the tube is complete and bears all the ten stamens characteristic of this group; in others, e.g. Pea, Bean, the tube is incomplete, being split along its posterior edge and carrying only nine of the stamens, the tenth being inserted directly on the receptacle just above the split.

Zonal growth at the base of the calyx, the corolla, and the andrœcium is thus responsible for a certain measure of cohesion between their members. Frequently it also happens that the primordia of petals and stamens, at first distinct, later continue their development from a common zone of growth. In this way petal-lobes and stamens are raised up on a common tube; but the corolla tube may continue to grow after the elevation of the stamens, so that the latter appear as if inserted inside the corolla tube, whereas actually they grew up along with the tube. Thus arises the condition of **epipetaly** or **epiphylly**—stamens fastened to corolla or perianth respectively. This condition indicates a state of higher evolutionary development in floral construction than that in which the stamens are independent of the corolla. Epipetaly is a constant feature of the higher families in both Dicotyledons and Monocotyledons, and together with sympetaly forms an important criterion in classification.

The stamens in the Dandelion family (*Compositæ*), in addition to being inserted within the corolla or perianth tube, also show lateral cohesion between the anthers themselves, so that they form an anther-tube which is supported by the free but epipetalous filaments. The anthers are said to be **syngenesious**; this condition is characteristic of the *Compositæ* (fig. 60).

The primordium of the stamen, as stated, begins its development as a small somewhat flattened cylinder of tissue projecting from the receptacle. By the early appearance of two median and opposite grooves the cylinder soon becomes bilobed, and in most cases each lobe again develops a lateral groove, so that the typical anther finally becomes four-lobed along its entire length (fig. 7, J, K).

Within each of the four lobes pollen is developed, and the term

pollen-sac is applied to each lobe and its contents. A certain amount of sterile tissue in the centre of the anther, serving as a supporting axis or columella, is known as the **connective**; in this region there arises a vascular strand which conveys food supplies to the developing anther and pollen.

The pollen escapes from the anther usually by two longitudinal slits which appear one at each side, in the lateral grooves. This disruption in the anther wall also extends into the partition between the pollen-sacs in each lobe; the two sacs on each side are thus put into communication and they discharge their pollen into the same fissure (fig. 28). The fissures in the anther wall may face either the interior of the flower, when the dehiscence is said to be **introrse** (fig. 23) or the exterior, when it is **extrorse** (fig. 27). Such directed discharge of the pollen has an important bearing on the method of pollination, and is determined by the shape of the anther. When the broader side of the anther faces the exterior of the flower, dehiscence is introrse; when it faces the interior, extrorse.

Dehiscence of the anther is controlled by specialized fibrous cells situated principally in the hypodermal layer. The mechanism of dehiscence is described in connexion with the development of the pollen-sacs and their contents (p. 72).

(*d*) The Gynœcium

The members of the gynœcium or pistil are called carpels. A flower which possesses one carpel or several carpels which are free from one another is said to be **apocarpous.** If the carpels are joined together the gynœcium is **syncarpous.**

The carpels are the most important of the floral members, for they bear the ovules, the future seeds. In general, the ripened carpels with their seeds constitute the **fruit.**

The similarity of a carpel to a foliage leaf is only discernible in the more primitive types of flowers, as in the *Ranunculaceæ*, where the carpels are free (fig. 11, C to E), or where the gynœcium consists of a single carpel (monocarpellary) as in the Garden Pea (*Pisum sativum*), or the Lupin (*Lupinus polyphyllus*) (figs. 3, 49) in the family *Leguminosæ.* The carpel of the Pea, for instance, is familiar in its fruiting condition as the pod containing the seeds (peas). The pod may be compared to a simple leaf folded along its midrib, and when the leaf margins meet and fuse together, a chamber or **loculus** is formed containing the seeds. The fused margins are called the **ventral suture** of the carpellary leaf, and along a ridge of tissue in this region known as the **placenta** the ovules are borne. The midrib, which is outside the folded carpel, is called the **dorsal suture,** though, of course, this does not imply any joining of parts to form it, for it is merely a convenient name to distinguish the " back " of the carpel from the true suture on the ventral side.

Thus far an attempt has been made to build up the carpel on the principle of a folded leaf. It must, however, be clearly stated that though the carpels start as primordia on the receptacle in the same way as sepals and petals, they do not become leafy expansions like these members.

The carpellary primordium originates as a small horseshoe-shaped protuberance which has its open side facing the apical meristem of the receptacle (fig. 7, H). The single carpel of the Pea or Lupin starts in this way. It grows forward as a narrow tube open along one side but tapering towards the apex (fig. 3, A to C). During its elongation the tube gradually closes in from the base and the sealed side is now called the ventral suture of the carpel. The space thus enclosed is called the loculus of the carpel. When the carpel becomes closed it extends forward by apical growth, forming a more or less solid projection, the **style,** which narrows towards its apex but finally expands to form the terminal **stigma.** The length and thickness of the style and the nature of the stigma vary considerably in different types of flowers. In some species (e.g. *Primula*) there are short-style and long-style forms. In the Buttercup or Celandine there is hardly any stylar prolongation and the top of the carpel is merely expanded into a stigmatic papillose lobe. In a few cases, e.g. Strawberry (*Fragaria vesca*), Lady's Mantle (*Alchemilla vulgaris*) of the *Rosaceæ* family, the style is developed from the side of the carpel.

The carpellary midrib is at the curve of the horseshoe primordium and it is furnished with vascular tissue from the receptacle. As the growth of the carpel proceeds, lateral veins from the midrib extend in all directions to ramify within the tissues of the carpellary wall in

Fig. 11. *The Apocarpous Gynœcium.* Diagrammatic.—A, single carpel, as of the Pea, cut across to show the unilocular ovary, midrib or dorsal suture, and fused margins or ventral suture where the ovules are attached to the placental ridge in marginal placentation. B the same opened along the ventral suture, showing the ovules attached to the carpellary margins. C the typical apocarpous gynœcium, as of *Caltha* (fig. 39, E), showing five free carpels with their ventral sutures directed inwardly. D the same in transverse section. E carpel of Buttercup incompletely closed; note absence of a style. F the same completely closed, forming a unilocular ovary with a single anatropous ovule in basal placentation. G carpel of Rose with long hollow style terminating in lobed stigma and with one or two anatropous ovules in pendulous placentation. H carpel of Bramble with long style and blunted stigma; the unilocular ovary contains two ovules in pendulous placentation. I carpel of Strawberry with style attached laterally; anatropous ovule in basal placentation.

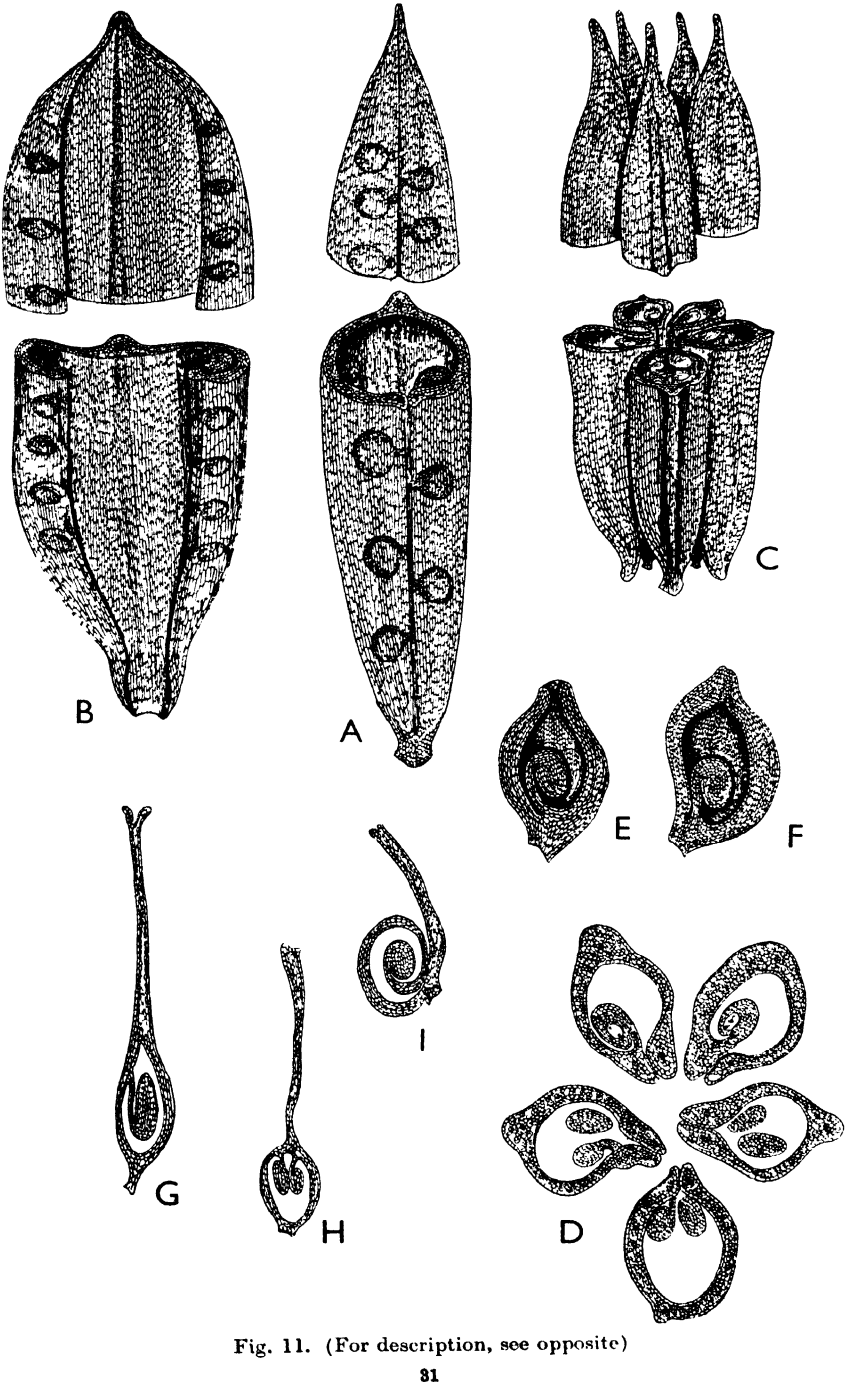

Fig. 11. (For description, see opposite)

much the same manner as they do from the midrib into the mesophyll of the foliage leaf. The carpellary veins are particularly prominent at the ventral suture, for it is necessary to have a vascular supply in this region to nourish the developing ovules along the placenta. The ground tissue of the carpel, especially in primitive forms like *Caltha* (fig. 32), often shows an intercellular system of air-spaces and stomata, especially around the sutural regions; such features are strongly reminiscent of the structure of an ordinary foliage leaf.

Parallel with the sealing of the carpel at the ventral suture (fig. 3, C), or even earlier (fig. 29, A), the **ovules** arise as minute primordia along the placental ridge. In carpels which contain only a single ovule, as in the Buttercup and Celandine, the same sequence of development is observed as in the monocarpellary pistil of the Pea or the Lupin, described above, and the fusion at the ventral suture can be seen as a groove which is continued into the apex as a two-lipped stigma (fig. 1, G). In the Buttercup and Celandine the solitary ovule is inserted at the base, and the ovule is said to be in **basal placentation**; in the closely related Wood Anemone (*Anemone nemorosa*) (fig. 38, E) the single ovule (there are frequently other, smaller aborted ones) hangs from the top of the ovary cavity in **pendulous** placentation.

The conditions of free and fused carpels, Apocarpy and Syncarpy respectively, have already been mentioned (p. 29); closer attention must now be devoted to these features in connexion with carpellary development and placentation. In the case of the apocarpous gynœcium consisting of more than one carpel, as in the Buttercup, &c., it need only be stated that development of each carpel takes place along the same lines as those described above for the monocarpellary gynœcium. The free carpels have a definite orientation with respect to one another, the ventral sutures being all directed inwardly towards the apex of the receptacle (fig. 11, D).

The carpels, usually the last members of the flower to arise, thus come to occupy the apex of the receptacle. The carpels are said to be **superior** when the other floral members are inserted below them. This position may be retained whether the carpels are free or joined. In more advanced types of floral construction than those described above, however, the growth of the receptacle may be so modified that it becomes a hollow, cup- or flask-shaped structure, within which the carpels are accommodated. In such advanced types, the gynœcium is said to be **inferior** to the other floral members, but only if the receptacle is completely closed over the carpels.

As the development of the inferior syncarpous gynœcium is considered in greater detail in connexion with advanced floral construction (p. 41), the following account deals with the development of syncarpy in the superior type of gynœcium. We have seen that the carpels appear on the receptacle as a number of distinct horseshoe-shaped primordia; they are symmetrically arranged around the apex of the receptacle and arise very close together, with their open ventral sutures facing the apex. After a brief period of independent growth, the horseshoe primordia are raised by a common tubular extension at their bases. Thus the primordia become linked together in the same way as sepals or petals are joined to form a gamosepalous calyx or sympetalous corolla. At a very early stage, therefore, the syncarpous gynœcium consists of a short tube or cup on the edge of which are the original protuberances of the primordia. (In some types, e.g. *Viola*, *Primula*, the gynœcium from the very start begins as a shallow cup.) In conformity with the horseshoe shape of the several primordia, the carpellary tube assumes a lobed contour, which is frequently preserved in the mature gynœcium. Thus the number of lobes in the wall of a syncarpous pistil is often a reliable indication of the number of carpels composing it.

When the upward projection of the tubular, fused carpels is nearly complete, the tapering orifice is finally closed by the tips of the lobes coming together. Although as many ovaries as there are carpels are involved in the syncarpous gynœcium, it is the custom to refer to the whole syncarpous structure as a **simple ovary**, irrespective of the number of carpels composing it.

The styles of the carpels develop by apical growth from the lobed tips at the apex of the ovary. In some types, e.g. the Tulip (fig. 12, F), the tips expand almost immediately into three stout ridges which become the papillose stigmas of this flower. In the Primrose (fig. 12, K) and Violet (fig. 42, F), the tips of the carpels merge into a single broad knob which is elevated above the ovary on a slender pillar or style. The extension of the carpellary lobes by apical growth and the degree of fusion between the lobes to form styles and stigmas vary considerably in different species or even in the same species of plant. When the sealing of the syncarpous carpellary tube is complete, a common procedure is for the tips of the lobes to grow forward independently of one another to form free styles each terminating in its own stigma, as in the Stitchwort (*Stellaria Holostea*) (fig. 12, G) and Red Campion (*Lychnis dioica*) (fig. 12, I): in these cases a count of the styles gives the number of carpels in the gynœcium. Sometimes, however, accidents of growth happen whereby two or more styles become joined (adnate) so that the number of free styles is not always a safe criterion of the number of carpels in a syncarpous gynœcium. In the flowers of the Grasses (p. 234) the gynœcium consists of a single carpel, yet the style is divided and profusely branched into a system of feathery stigmas.

Again, in the upward projection of the lobed carpellary tips their free condition may be very brief, so that when early fusion takes place below them, the free terminations are eventually raised up on a common stylar column. Thus arises the " split " condition of the style in such flowers as the Apple (*Pyrus Malus*) (fig. 53, A), the Foxglove (*Digitalis purpurea*) (fig. 58, C), the Dandelion (*Taraxacum officinale*) (fig. 60, D), &c. In a few cases the styles do not develop from the lobed tips of the carpels; for example, in the bicarpellary gynœcium of the family *Labiatæ*, the style grows up from the base (gynobasic) along with and between the carpels.

In flowers which are pollinated by insects, the stigmatic surfaces are usually papillose and sticky to receive the adhesive pollen; in wind-pollinated flowers, the stigmas are richly branched (" feathery ") and their terminations are highly glandular for the reception of the dry, wind-borne pollen.

It is interesting to note that the loculi of the ovary in many types of flowers are continued into the styles as canals which may extend the whole way up to the stigma, e.g. Violet (fig. 42, D), or only a part of the way, e.g. Primrose (fig. 55, E). The stylar canals are lined with mucilaginous hairs which facilitate the passage of the pollen-tubes on their way to fertilize the ovules. In the higher-evolved types of flowers, however, the styles are usually solid and the descending pollen tubes travel mostly by the intercellular spaces (fig. 31).

(*e*) Syncarpy and Placentation

The mode of attachment of the ovules (**placentation**) in syncarpous ovaries varies according to the extent to which the ventral sutures grow inwards into the ovary cavity.

Fig. 12. *The Syncarpous Gynœcium* Types of Ovules. Diagrammatic.—A, three carpels with convergent ventral sutures fusing together as they grow forward to form a unilocular syncarpous gynœcium as in B. C convention used in floral diagrams; note midribs and infolded ventral sutures, showing three parietal placentæ in the unilocular ovary. D twisted syncarpous ovary of an Orchid with parietal placentation (figs. 70, 71). E bicarpellary gynœcium of Shepherd's Purse cut across to show the two parietal placentæ; the ovary becomes bilocular by the formation of a false septum (cf. fig. 18). F tricarpellary gynœcium of the Tulip with three-lobed stigma but no style (fig. 65). G same of Stellaria with three free styles (fig. 43). H conventional section of F showing trilocular ovary with ovules in axile placentation (fig. 29). I the five-carpellary gynœcium of Red Campion, with five free styles. J transverse section of same showing a unilocular condition of the ovary resulting from the breakdown of the five septa opposite the ventral sutures; the placentation of the ovules is therefore central. K five-carpellary gynœcium of Primrose with single style terminating in knob stigma. L transverse section of same showing free-central placentation (fig. 16). M erect or orthotropous ovule. N curved or anatropous ovule. O curved and bent or campylotropous ovule; note relative positions of micropyle *m*, funicle *f*, and chalaza *ch*; in all cases the " egg-apparatus " within the embryo-sac faces the micropyle.

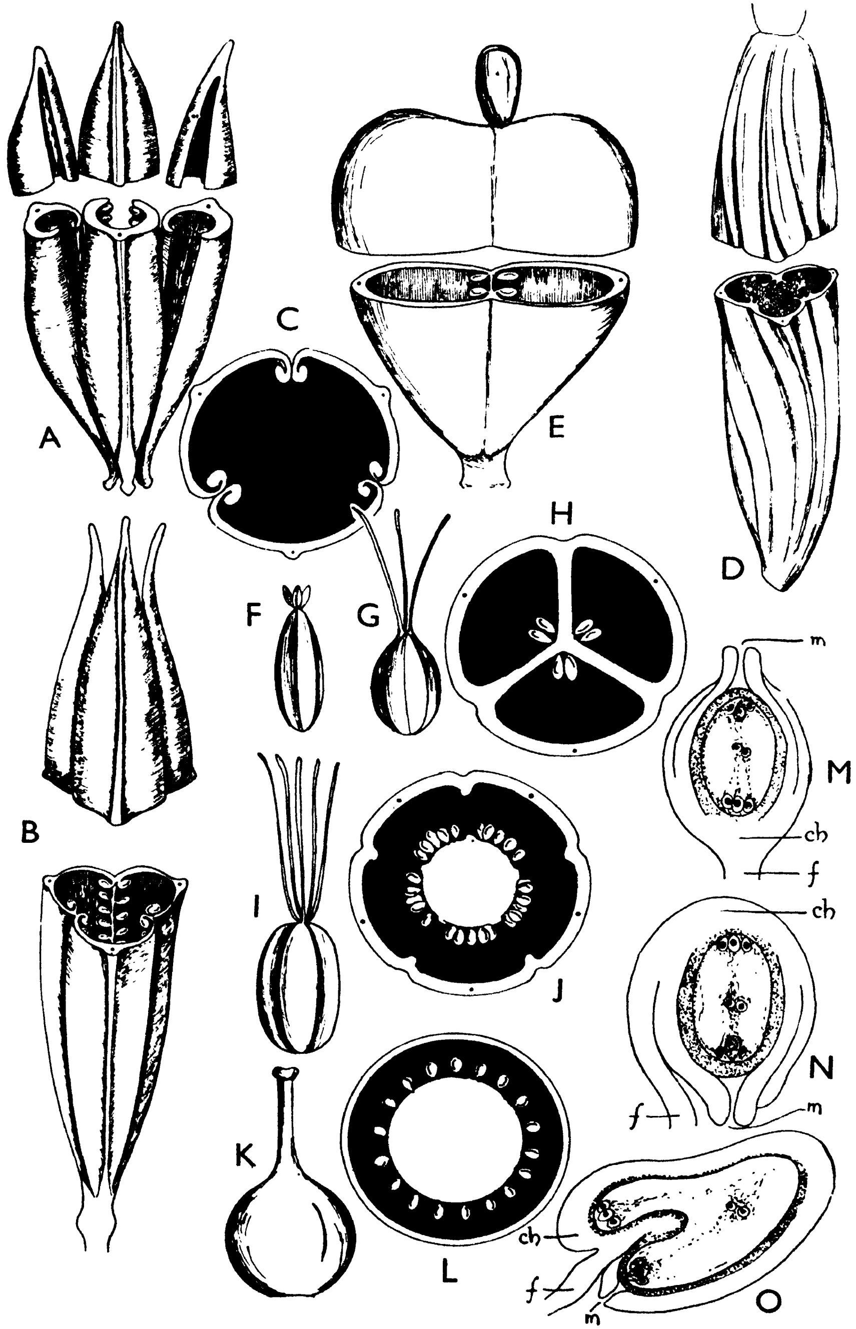

Fig. 12. (For description, see opposite)

If the ventral sutures do not reach the centre, so that the ovary remains unilocular, the placentæ appear as ridges on the internal wall and the ovules thereon are said to be in **parietal** placentation (fig. 12, C, D). This arrangement is also sometimes called **marginal**, but this term is more applicable to the mode of placentation in a monocarpellary pistil, as in the Pea (fig. 11, A) or in the single carpels of an apocarpous gynœcium, as in *Caltha*, &c. (fig. 11, C), which contain numerous ovules along the ventral suture.

The type of placentation in the bilocular gynœcium of the Wallflower family (*Cruciferæ*) is complicated by the formation of a septum which divides the original single loculus into two compartments; but as the dividing wall is formed by the two placental ridges growing into and meeting in the loculus *after* the ovules are laid down, it is a false partition, and the ovules, being still on the carpellary wall, are in parietal placentation (figs. 12, E, and 18). In the ovary of the Orchis, the three parietal placentæ develop a number of irregular lobes or ridges on which a very large number of minute ovules are formed (figs. 12, D and 70, 71).

A mode of placentation known as **axile** is very common. It results from further ingrowth of the ventral sutures which meet and fuse at the centre of the ovary; the ovary is therefore divided into as many compartments or loculi as there are carpels (figs. 12, H and 15, 17. 19). The axile placenta often grows into a massive tissue almost filling the loculi, and bearing numerous ovules all over its surface, e.g. Foxglove (fig. 19), Potato (fig. 17).

In the Stitchwort family (*Caryophyllaceæ*), the five, or fewer, carpels are united during early development in axile fashion but the gynœcium may later become unilocular by the breaking down of the partitions. The ovary thus appears to have a central axis which has no connexions with the carpellary wall, but closer examination reveals remnants of the broken septa on the wall as well as on the placental axis (figs. 12, I, J; 43, G). The ovules occupy the central axis and the placentation is **central.**

Finally, a form of placentation which arises in a different way from all the foregoing is found in the Primrose family (*Primulaceæ*). The five-carpel ovary of this flower (figs. 12, K. L and 16) is perfectly smooth-walled, within and without, and shows no indication of the ingrowth of ventral sutures to form placentæ in the normal manner. A vertical section of the ovary (fig. 55, E), however, shows that the placenta arises from the base of the ovary, and it projects into the loculus as a massive cone of tissue bearing numerous ovules reaching almost to the base of the style. This placentation is known as **free-central.**

The ovules of flowering plants show great uniformity of structure and contents. At this point we shall describe only the mature structure of the ovule. A typical ovule consists of an ovoid mass of tissue, called the **nucellus,** which is covered by one or in some cases two coats called the **integuments.** The latter invest it completely except for a small portion at the apex where a small pore or **micropyle** is left. The ovule is finally raised on a short stalk or **funiculus** which is attached to the ovule at its broadest basal part, the **chalaza.** A vascular strand from the placenta of the carpel passes into the stalk of the ovule and distributes itself into the chalazal region.

There are three somewhat distinctive types of ovule. If the ovule is straight, having the stalk, chalaza, and micropyle in line, it is said to be **orthotropous.** The commoner type of ovule called **anatropous,** however, curves over during development, so that its micropylar end comes to lie alongside the funiculus. A third kind, the **campylotropous** ovule, is also curved, but its chalazal part projects backwards to lie alongside the stalk, which then appears between chalaza and micropyle (fig. 12, M to O).

The interior of the mature ovule, in longitudinal section, shows the presence within the nucellus of a large oval cell, the **embryo-sac** or **megaspore** (also called the macrospore), situated close to and directly below the micropyle. Prior to fertilization the typical embryo-sac contains eight nuclei. Three of these, collectively called the **egg-apparatus,** are close together and occupy the micropylar end of the sac; they consist of a central **egg** or **ovum** and two **synergidæ,** one on each side. At the opposite, chalazal, end is another group of three nuclei called the **antipodals,** and at the centre is a pair of **polar** nuclei, which may, however, be found already fused together to form the **definitive** nucleus. All these nuclei are invested with the cytoplasm of the embryo-sac, but around each of the antipodal nuclei there is a thin cellulose wall.

The sporangia of the flower, namely, the pollen-sacs within the anther and the ovules within the carpels, have thus far been described in outline only. Their development, including the formation of the sexual cells or gametes, is considered in greater detail in Chap. V.

CHAPTER IV

Floral Construction and Symmetry

(*a*) Construction

There are three fundamental lines of development in floral construction, (*a*) **hypogynous,** (*b*) **perigynous,** (*c*) **epigynous.** They are determined by certain modifications in the mode of growth of the floral axis or receptacle.

When the carpels, free or joined, appear at the end of a receptacle which is conical, e.g. Buttercup (fig. 2), or dome-shaped, e.g. Wallflower (fig. 41), or flat, e.g. Violet (fig. 42), and the other floral members are inserted, in turn, below the level of the carpels, the flower is said to exhibit **hypogyny** (fig. 13, A to C). This is clearly seen in the types just named, where the stamens, petals, and sepals are attached to the receptacle independently of one another. The term, however, is also applicable to sympetalous flowers such as the Primrose (fig. 55), Foxglove (fig. 58), Potato (fig. 56) which have epipetalous stamens, for despite the insertion of the stamens on the petals in these flowers, the critical factor in the determination of hypogyny in sympetalous types is the seat of insertion of the corolla-tube, which in the above-named examples is immediately below the gynœcium. In hypogynous flowers the gynœcium itself is said to be **superior,** that is, the carpels occupy the apex of the receptacle.

A second form of floral construction is that of **perigyny** (fig. 13, E). It is well shown by members of the Rose family (*Rosaceæ*) in which, again, the receptacle assumes various shapes. In the first instance, illustrated by the Blackberry or Bramble (*Rubus fruticosus*) (fig. 50, G), or

Fig. 13. Development of *Hypogyny, Perigyny, Epigyny,* from a basic type A.—The series A–B–C shows the derivation of hypogyny, the floral members in order from the outside being the receptacle *r* (shaded); calyx *k*; corolla *c*; andrœcium *a*; and gynœcium *g*, at the apex, thus making the ovary superior. The series A–D–E illustrates the derivation of perigyny, showing the zonal growth *z* from the receptacle raising the calyx, corolla, and andrœcium, the ovary being still superior. The series A–F–G shows transition from perigyny to epigyny, as in the Apple flower (fig. 53); the receptacle is incorporated with the wall of the gynœcium and the carpels are now enclosed, rendering the ovary inferior; the floral members are inserted on an epigynous rim. The series A–H–I shows advanced epigyny, as in the *Compositæ* (fig. 10); zonal growth below the corolla and andrœcium has formed a corolla-tube *ct*; the walls of the receptacle and carpels are undifferentiated.

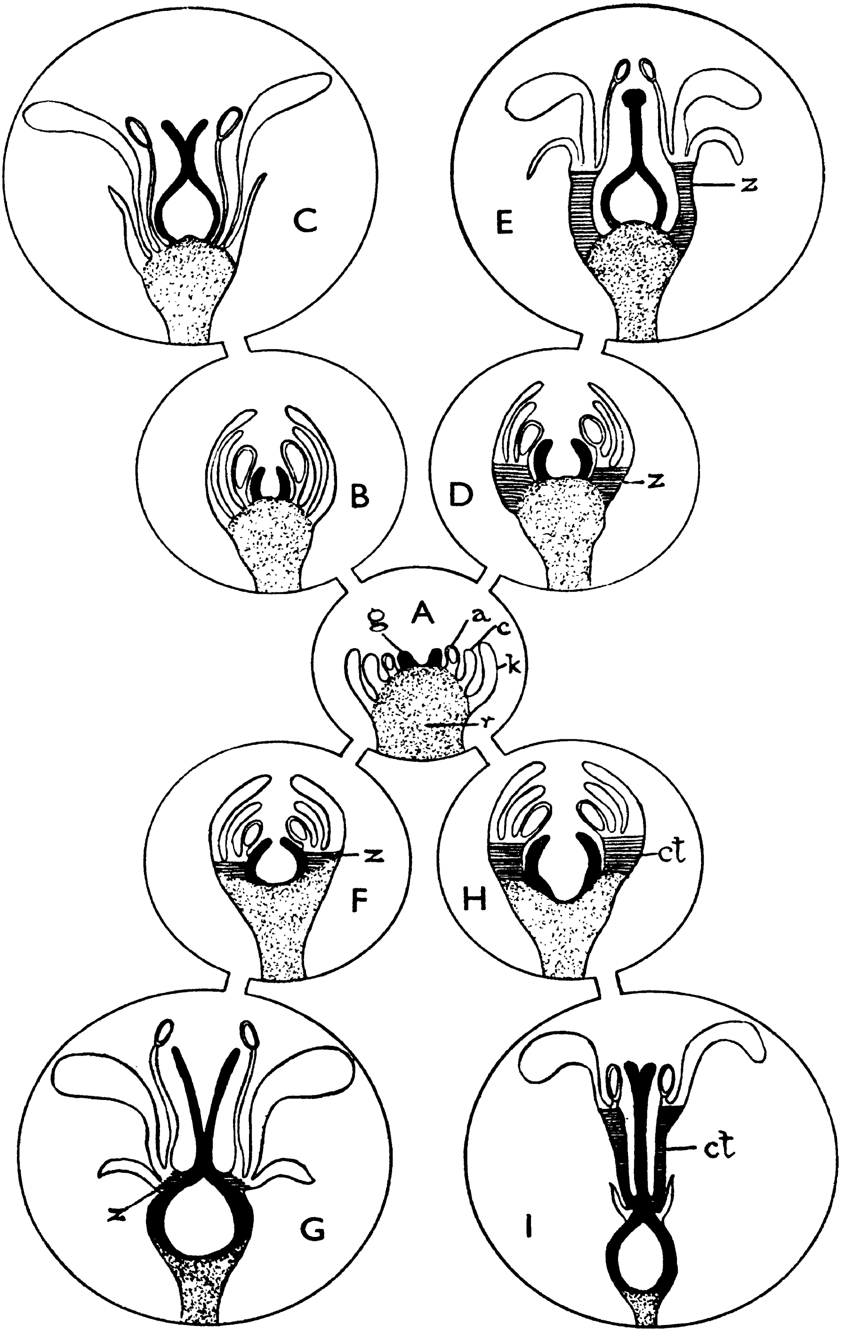

Fig. 13. (For description, see opposite)

the Water-avens (*Geum rivale*) (fig. 51), the perigynous condition may be derived from a conical or dome-shaped receptacle by expansion around its base to form a rim or concave flange. During this development the primordia of the sepals, petals, and stamens are carried outwards on the edge of this lateral extension of the receptacle, but the carpels are formed on the central projecting part of the receptacle. In these flowers the carpels appear isolated and surrounded, at an appreciable distance away, by the other floral members. The relative position of these members *around* the gynœcium is described as perigynous. As in the hypogynous construction, the carpels are still **superior,** for they occupy the apex of the receptacle. Another type of perigyny is seen in the Blackthorn (*Prunus spinosa*) (cf. figs. 9, 13, E, and 52). Here, growth of the receptacle at its organic apex is greatly retarded, but extends actively around its margin until finally a cup-shaped structure is formed. The sepals, petals, and stamens are again carried outwards during their development, so that they appear around the edge of the cup. The gynœcium (consisting in *Prunus* of a single carpel) is formed at the original apex of the receptacle, and therefore occupies the base of the cup. Despite the seeming elevation of the outer floral members above the level of the carpel, the latter is still "superior", for the receptacular cup remains open. A third instance of a more pronounced form of perigyny is shown by the Rose (*Rosa canina*) (fig. 50, C). The receptacle develops in the same way as that of the Blackthorn, but in the Rose it becomes deeper and narrower at the top, like a flask. The organic apex of this deep receptacle is again within the base of the flask, and here the numerous free carpels are laid down. During their formation, the upward growth of the flask carries some of the carpels up so that they appear on the sides of the hollow receptacle. The carpels put forth long styles ending in capitate stigmas which protrude at the narrow orifice of the receptacle. It is important to note that as long as the receptacle of a perigynous flower is open to the exterior by an opening, however narrow, the carpels are still superior.

It is not always easy to distinguish slight perigyny from hypogyny, especially when the receptacle is flat or only faintly concave, as in numerous types of the family *Leguminosæ.* Close examination of such flowers as the Broom (*Sarothamnus scoparius*) (fig. 47, G), Lupin (*Lupinus polyphyllus*) (fig. 49, E), &c., will show, however, that the insertion of the staminal tube, characteristic of this family, is carried a little away from the level of the carpellary base.

A third type of floral construction is known as **epigyny** (fig. 13, G, I). This advanced feature is so closely bound up with the development of the carpels themselves that its association with a cup- or flask-shaped receptacle is not so evident, particularly in the highest-evolved types of epigyny, e.g. in the family *Compositæ*. The nearest approach to the flask receptacle of perigyny, as in the Rose, occurs in the Apple group (*Pomoideæ*) of the Rose family. Thus in the flower of the Apple (*Pyrus Malus*) (figs. 13, A, F, G, and 53, A) the receptacle forms a deep cup, and the five carpels inside it are not only fused together in development in the manner of a syncarpous gynœcium, but the tissues of their outer walls are also merged into those lining the receptacular cup. The ovaries of the carpels are completely closed in and fused with the receptacle; the five styles (fused at their bases) protrude at the top, but there is no opening at this part of the receptacle. The flower is accordingly epigynous, for the other floral members are now situated on top of a *closed* receptacle. (Actually, in the Apple the stamens, &c., are attached to the rim of a shallow epigynous cup (fig. 53).) This fusion of receptacle and carpels is so intimate that the combined structure is called an **inferior** ovary. This term implies that the gynœcium is now definitely *below* the other floral members.

The development of epigyny in the highly evolved *Compositæ* is somewhat different (fig. 13, A, H, I) from that in the Apple. During the formation of the tubular sympetalous corolla, the receptacle becomes more and more concave, ultimately assuming a flask shape. The only indication that two carpels, characteristic of this family, are being laid down is the presence of two opposite and semicircular primordia at the narrow orifice of the receptacular flask. These grow upwards with their flat surfaces close together, but they soon fuse from the base upwards to form a single style, the double nature of which, however, is preserved at its apex in the closed but bifid stigma. In the flowers of the *Compositæ*, therefore, the two initial stylar protuberances are the only indication of the presence of the two carpels, for the latter are indistinguishable from the receptacle. Indeed, the receptacular flask, now sealed by the stylar fusion, constitutes the bicarpellary gynœcium; it encloses a single ovary-cavity from the base of which arises a single ovule (fig. 10).

(*b*) Symmetry

The disposition of the floral whorls in the general architecture of the flower, together with the number and distribution of the members composing each whorl, plays an important part in the general symmetry of the flower. Moreover, these features, in conjunction with the general floral construction as outlined above, form a useful basis of classification of the flowering plants. To this end, a study of the plan of a flower or, better, a transverse section of the flower in a young condition in the bud, is very helpful. The following six types of floral symmetry are considered from this point of view.

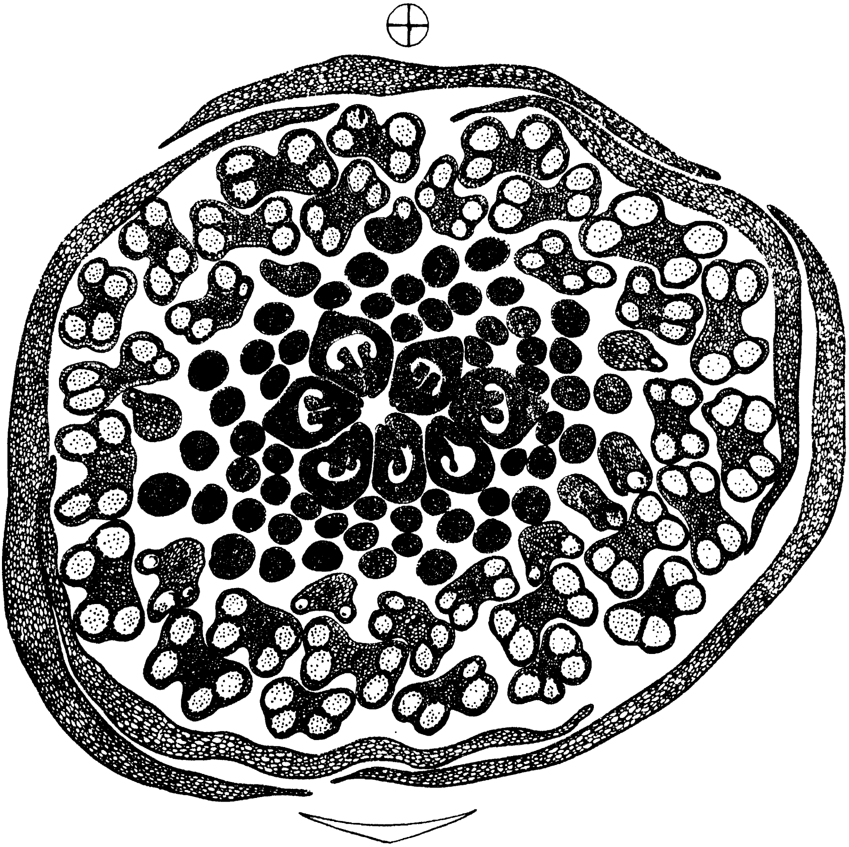

Fig. 14. Floral Bud of *Caltha palustris*, Marsh Marigold.—Transverse section. The investing five members are those of the calyx. There are about a hundred stamens in a spiral, in ranks five deep; the seçtion passes through the anthers of the outer divergent stamens (showing extrorse dehiscence) and across the filaments of the inner stamens. The apocarpous gynœcium consists of a variable number of carpels.(about seven), having their " midribs " or dorsal sutures directed towards the outside and their ventral sutures inwards; note the ovules in marginal placentation. All the parts of the flower are built on a spiral plan. (Cf. fig. 39, F.)

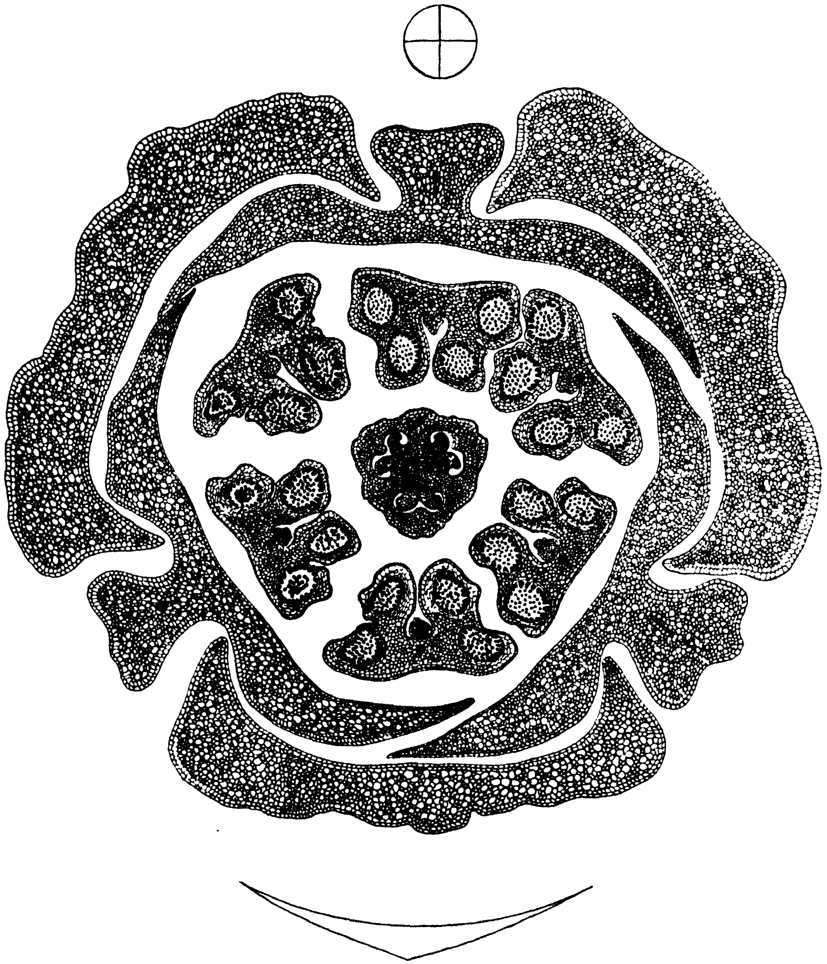

Fig. 15. Floral Bud of *Lilium*.—Transverse section. The typical Monocotyledon flower. Perianth in two whorls of three segments. Androecium in two whorls of three stamens each; note that the broader part of the anthers is directed towards the perianth and dehiscence is therefore introrse. The central syncarpous gynoecium consists of three carpels with trilocular ovary showing axile placentation.

1. The Marsh Marigold (*Caltha palustris*) (figs. 14 and 39, D).

In primitive flowers of this type, which also includes several other members of the *Ranunculaceæ*, e.g. the Christmas Rose (*Helleborus niger*) and Clematis (*Clematis Vitalba*) (fig. 38, G), all the floral organs are arranged on a conical receptacle in a continuous **spiral.** This flower, moreover, shows such a large number of stamens in comparison with sepals and carpels that it is difficult to make out any prescribed arrangement of its parts. The sectional view of the bud (fig. 14) shows that the five sepals (the number varies), which overlap at their margins, are equidistant. The hundred or more stamens follow in close succession along some five turns of a spiral, the remainder of which is occupied by about five to fifteen free carpels. Such a flower may therefore be divided into identical halves in several planes of median vertical section. It is therefore said to possess **radial symmetry,** or, as stated on p. 24, the flower is regular or actinomorphic. The flower of the Buttercup with its well-defined petals as well as sepals, however, differs from the above types in that the calyx and corolla arise independently in separate **whorls,** but the stamens and carpels follow the same primitive spiral arrangement as in *Caltha.* The Buttercup is therefore **hemi-cyclic,** but again possesses radial symmetry.

2. The Lily (*Lilium* sp.) (fig. 15). (Cf. *Tulip*, fig. 65.)

The more advanced types of flowers follow the system begun in the Buttercup of providing separate whorls for the different members, and are said to be **cyclic.** Moreover, there is a marked tendency towards a reduction in the number of stamens and sometimes of carpels also. The number of members in each whorl is frequently constant, three, four, or five being a common number in specified types; such flowers are said to be **trimerous, tetramerous,** or **pentamerous,** respectively. A very common arrangement in the flowers of both Monocotyledons and Dicotyledons is the provision of five whorls (**pentacyclic**), two for the floral envelopes, two for the stamens, and the central whorl for the carpels. Other dicotyledons with four whorls, owing to the presence of only one staminal whorl, are said to be **tetracyclic.**

The Lily illustrates a cyclic trimerous arrangement which is typical of the flowers of Monocotyledons. The six perianth lobes arise in two whorls of three members each, and likewise the six stamens in the succeeding two whorls, and finally the fifth whorl is occupied by the three carpels. Fig. 15 shows that the members of each whorl alternate with those of the next whorl. Thus the three stamens of the outer ring face the members of the outer perianth whorl; the inner stamens face the members of the inner perianth lobes; even the triangular

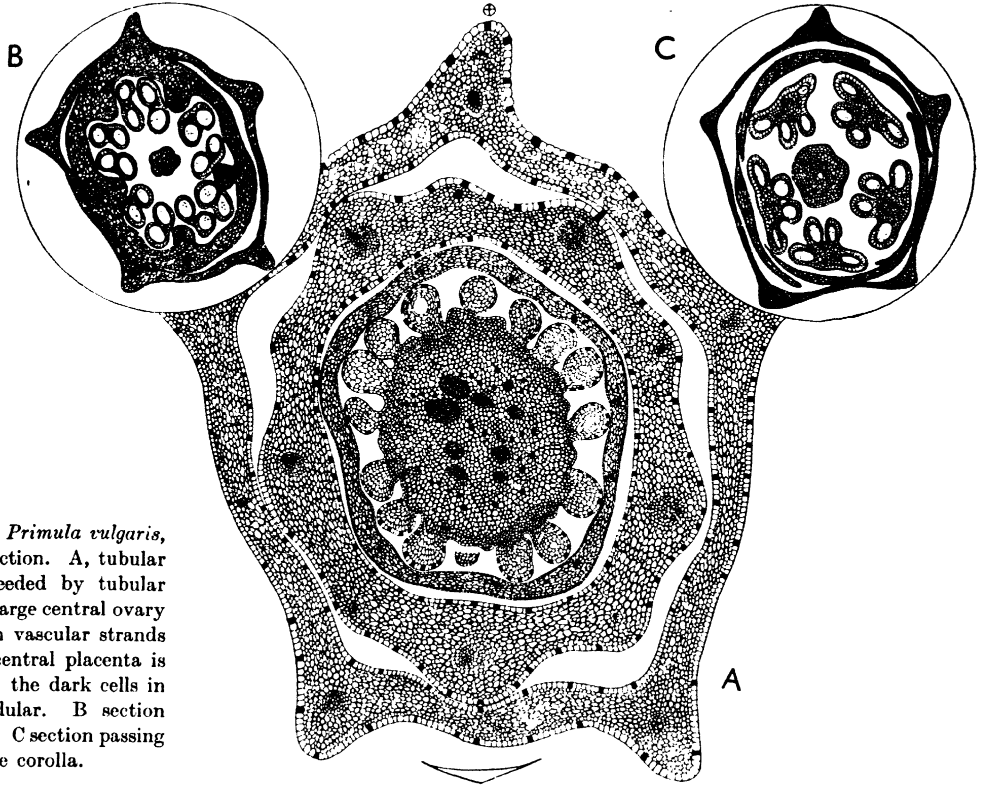

Fig. 16. Floral Bud of *Primula vulgaris*, Primrose. — Transverse section. A, tubular calyx of five sepals succeeded by tubular corolla of five petals; the large central ovary is lobed and there are ten vascular strands in its wall; the massive central placenta is free from the ovary wall; the dark cells in all the tissues are glandular. B section passing across the stamens. C section passing across the five lobes of the corolla.

outline of the gynœcium shows that its angles (the dorsal sutures) are definitely oriented so as to face the outer stamens. This flower exhibits perfect radial symmetry.

3. The Primrose (*Primula vulgaris*) (figs. 16 and 55).

The floral bud of the Primrose again exhibits remarkable radial symmetry. It is, however, fundamentally different from the monocotyledonous flower above and that of *Caltha* in that it is built on a five-member plan (pentamerous) which is typically but not exclusively that of dicotyledonous flowers. The outer ring forming the calyx is tubular (see fig. 55) but it still exhibits its origin from five sepal primordia, for the calyx tube is furnished with five teeth and it is also prominently five-ribbed. Similarly, the corolla (also tubular and composed of five petals alternating with the sepals) shows a spreading five-lobed condition indicating the number of petals. In the Primrose, however, there are not two whorls of stamens, only one ring of five being developed. Moreover, the position of this single staminal whorl appears to upset the principle of alternation of members in successive whorls, for these stamens actually face the petals. The explanation usually put forward is that an outer whorl of five stamens is suppressed. Finally, the gynœcium is also built on a five-member plan (though it is difficult to substantiate this fact, even by a developmental study); when the Primrose ovary becomes a fruit the dehiscence of the latter by five apical teeth no doubt indicates that the gynœcium consists of five carpels.

The omission of a complete staminal whorl from the Primrose does not, however, affect its symmetry, and this flower is again actinomorphic with radial symmetry.

4. The Potato (*Solanum tuberosum*) (figs. 17 and 56).

With the exception of the gynœcium, the flower of the Potato again presents a pentamerous condition. In considering problems of floral symmetry, however, it is customary to attach greater importance to the form of the corolla or perianth, together with the number and disposition of the stamens, giving less significance to the constitution of the gynœcium. These features are illustrated in the Potato flower, which shows seemingly perfect radial symmetry; but developmental study of the flower reveals that the partition dividing the two carpels cuts the antero-posterior plane *obliquely*, throwing the whole floral construction out of order, as it were. The orientation of the ovary, however, is considered to be of minor importance. The flower is

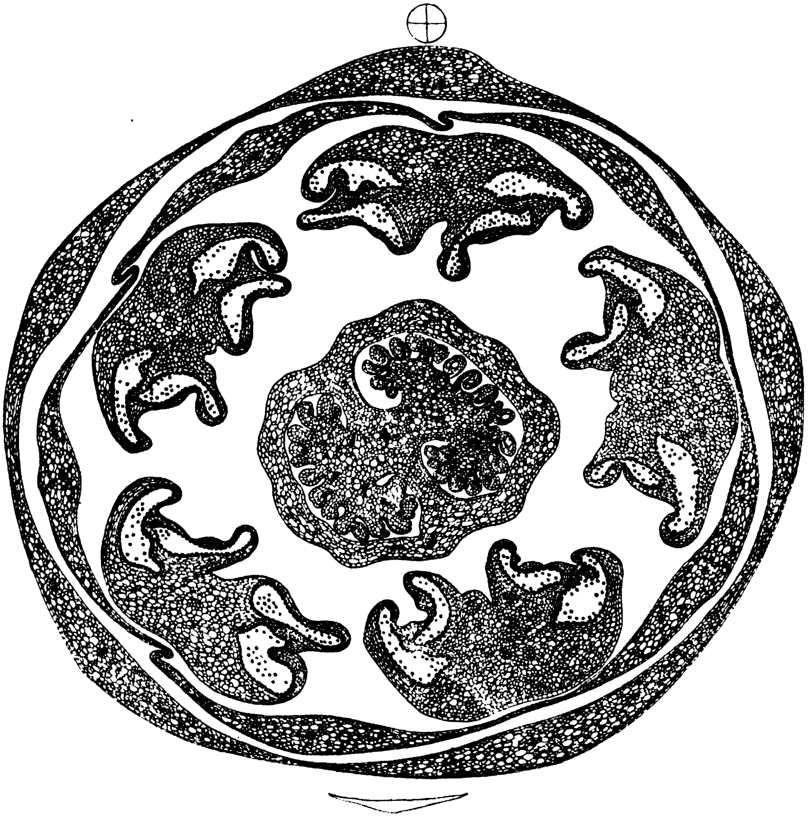

Fig. 17. Floral Bud of *Solanum tuberosum*, Potato.—Transverse section, showing radial symmetry but with oblique orientation of the gynœcium. The outer whorl consists of a five-lobed gamosepalous calyx; the next whorl is that of the five-lobed sympetalous corolla; the third whorl of five stamens alternates with the lobes of the corolla; the central, bicarpellary gynœcium is distinctive, for the placenta is obliquely placed in relation to the antero-posterior plane; the ovules are in axile placentation.

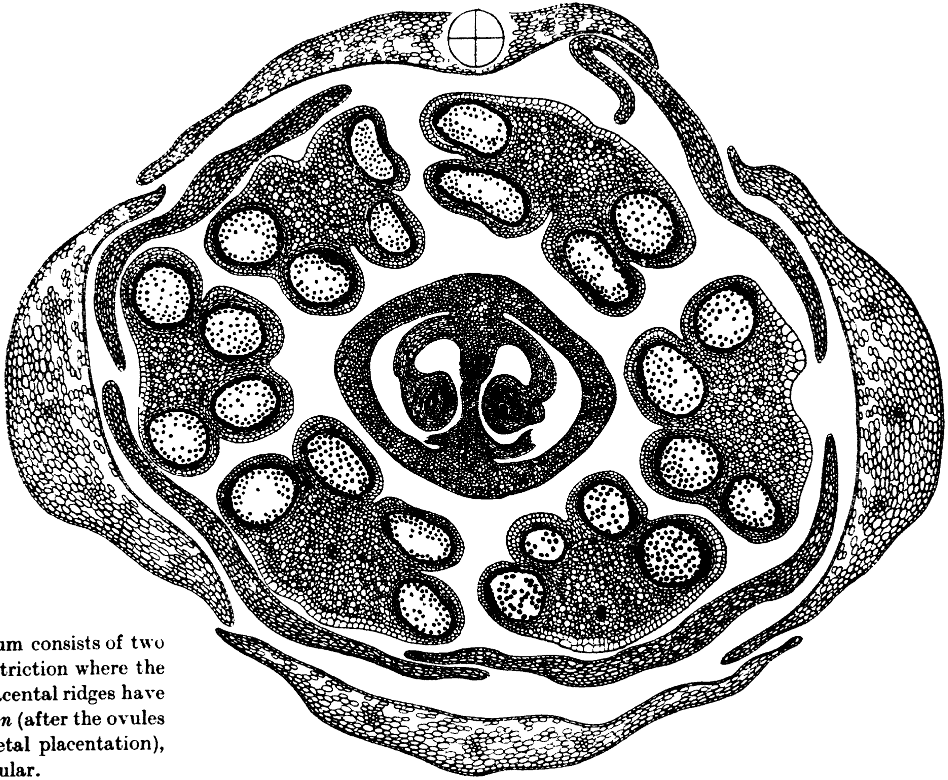

Fig. 18. Floral Bud of *Brassica Rapa*, Turnip. — Transverse section. Calyx in two whorls of two sepals each, the lateral sepals being broader or pouched; corolla in single whorl of four petals in a cross (cruciform). The andrœcium consists of two lateral stamens in the outer whorl and four antero-posterior stamens in the inner whorl. Centrally, the gynœcium consists of two syncarpous carpels; note constriction where the two ingrowing parts of the placental ridges have fused to form the *false partition* (after the ovules have been laid down in parietal placentation), thus rendering the ovary bilocular.

accordingly said to be actinomorphic with radial symmetry, on account of the regular disposition of the other floral members. Unlike the Primrose, the Potato flower is truly tetracyclic and the single staminal whorl is in correct orientation in relation to the corolla.

5. The Turnip (*Brassica Rapa*) (fig. 18). (Cf. *Wallflower*, fig. 41.)

The flowers of the family *Cruciferæ*, of which the Turnip is a member, show a remarkable uniformity of structure. The cruciferous flower appears to be built on a basis of two members in a whorl (**dimerous**). The calyx consists of two whorls of two sepals each; the outer pair stands in the antero-posterior plane, and the inner pair in the lateral plane, in correct alternation. The two inner sepals, however, are shaped differently from those of the outer; they are distinctly pouched or saccate at the base. The four petals are in a single whorl, and in order to preserve the dimerous condition prevailing in the calyx, it is stated that the four petals may have originated from the branching of two primordia; this view, however, is not sustained by a study of development. There are again two whorls of stamens; the outer whorl consists of two situated in the lateral plane, and the inner whorl is occupied by four taller stamens which stand in pairs, rather close together, in the median plane. The same theory of duplication by branching of two staminal primordia to produce the four inner stamens, is again put forward, but as in the case of the corolla the evidence is inconclusive. Finally, the gynœcium preserves the dimerous condition, and the two fused carpels have their dorsal sutures in the lateral plane. While the Crucifer flower shows great uniformity in its plan, the difference in the shape of the sepals in the two whorls, and the disposition of the six stamens in their respective whorls, show that there are only two planes of division, namely, the antero-posterior (median), and the lateral plane at right angles to this, whereby two symmetrical halves can be obtained. But the half flowers cut in one way are different from those cut the other way. This type of symmetry is known as **iso-bilateral**; but despite the inequality mentioned in the calyx and the distribution of the stamens, the flower is described as actinomorphic because of the even shape of the diagonally arranged (" cruciform ") petals.

6. The Foxglove (*Digitalis purpurea*) (figs. 19 and 58).

A final type of symmetry of frequent occurrence among the higher-evolved families of flowering plants is illustrated by the Foxglove (fig. 19). The corolla of this flower is widely tubular but compressed from back to front; moreover, the mouth of the corolla tube shows that the anterior edge projects as a three-lobed lip, whilst the posterior edge is distinctly notched into two lobes. Thus the five petals have become united to form a tube which, on account of its compression and the unequal projection of its anterior and posterior lobes, is symmetrical along one plane only, namely the antero-posterior or median plane. A striking feature of the Foxglove is the presence of only four out of the five stamens expected. The blank position is posterior, and the absence of the fifth stamen emphasizes still more the one plane of symmetry. The flower is said to possess **bi-lateral** symmetry and to be zygomorphic in the median plane. The principal feature of the flower which determines bi-lateral symmetry and zygomorphy, then, is the shape of the corolla.

(*c*) Distribution of the Sexes

In the great majority of flowering plants. stamens and carpels occur in the same flower, which is then described as **bisexual** or hermaphrodite. Flowers are **unisexual** when the stamens and carpels are in separate flowers; these are conveniently referred to as male or female, as the case may be. Again, the sexes may be variously associated in both inflorescence and plant. Staminate and carpellary flowers may be found together in the same inflorescence, as in Coltsfoot (*Tussilago*) (fig. 60), or the unisexual flowers, of either kind, may be found associated with bisexual ones, again in the same inflorescence, as in some members of the *Compositæ* and *Umbelliferæ* (pp. 217, 198). In some plants the male and female flowers are in separate inflorescences; when these occur on the same plant, the latter is said to be **monœcious** (e.g. Oak, Hazel, Maize), and **diœcious** if on separate plants (e.g. Willow, Poplar, Dog's Mercury, Red Campion). There is, however, no hard-and-fast habit as regards these conditions, for we may find unisexual inflorescences, completely of male flowers, or completely of female flowers, along with one or more inflorescences which are partly of male and partly of female flowers, all on the same plant (e.g. *Carex* sp., p. 229).

(*d*) Meiomery

The phenomenon of reduction in the number of parts in a flower, whether these are single members like petals or stamens, or complete whorls of members, is known as **meiomery.** There are all grades of reduction, extending from the suppression of a single member, to the complete disappearance, in some cases, of all the stamens, and in others, of all the carpels, and in some instances both stamens and carpels are absent. It is thought that all these phenomena have been brought about by evolutionary change.

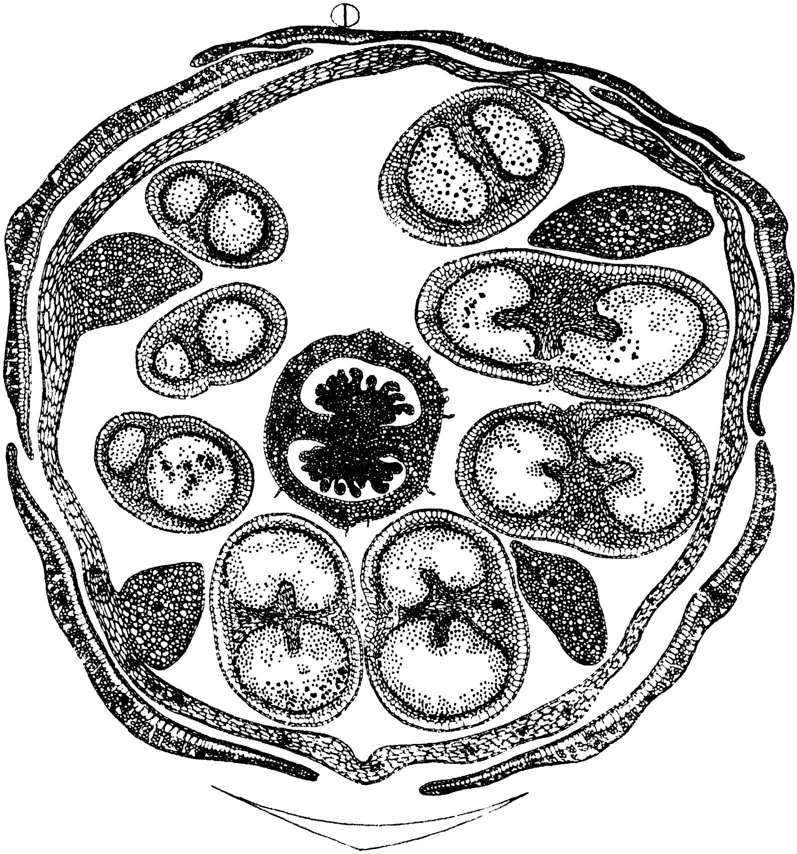

Fig. 19. Floral Bud of *Digitalis purpurea*, Foxglove.—Transverse section showing Bilateral Symmetry (*Zygomorphy*). Exterior whorl of five sepals; next whorl, the tubular corolla of five petals; the epipetalous protuberances are the filaments of the four stamens, the anther lobes of which are isolated in the section (the complete anther consists of the two lobes on either side of the cut filament); note blank space indicating absence of a fifth posterior stamen; centrally, the bicarpellary, syncarpous and bilocular gynœcium with a massive axile placenta.

An interesting "reduction-series" in the number of stamens is seen in certain flowers of the Foxglove family (*Scrophulariaceæ*). The basic number of parts in the flowers of this family is five, and the Mullein (*Verbascum Thapsus*) possesses the full complement of five stamens; in the Figwort (*Scrophularia nodosa*) (fig. 59, C) there are four stamens, but the position of the fifth stamen is occupied by an aborted stamen (staminode); in the Foxglove (*Digitalis purpurea*) (fig. 58) there are again four stamens, but here there is no sign of a fifth; finally, in the Speedwell (*Veronica Chamædrys*) (fig. 59, H) there are only two stamens.

In the flowers of the Red Campion (*Lychnis dioica*) (fig. 46), a member of the family *Caryophyllaceæ*, it is probable that reduction has gone so far as to cause these flowers to become unisexual. This species, as previously mentioned (p. 50), has two kinds of plants in which the sexes are separate, but it is interesting to note that there are distinct vestiges of stamens in the carpellary flowers, and in the staminate flowers the position of the gynœcium is occupied by a mere pointed structure.

Finally, there are certain flowers, termed **neuter**, which possess neither stamens nor carpels. Instances of neuter flowers are found in the *Compositæ*, where they occur in some types on the margin of the capitulum inflorescence, very conspicuous and brightly coloured, surrounding the other fertile flowers. No doubt they serve to attract insect visitors to the capitula (e.g. Cornflower, *Centaurea Cyanus*) (fig. 61, F).

(*e*) Pleiomery

In contrast with the above, there are numerous floral types which show an increase in the number of parts, or of floral whorls, as compared with the normal basic number which is usually given by the sepals and petals. This condition is known as **pleiomery.** Such increase is most commonly met with amongst the stamens. It may be brought about by a division of the original primordia, or it may possibly result from the development of additional primordia, as is most likely the case with the very numerous stamens in many types of the family *Rosaceæ* (figs. 50 to 53).

The familiar instances of *double flowers*, mostly in cultivation (e.g. Roses, Stocks), appear to have a preponderance of petals over the usual number found in the corolla of their prototypes. The extra petals arise almost exclusively at the expense of the stamens, but in extreme cases all the stamens and carpels may be replaced by petals.

(*f*) The Floral Diagram

A consideration of floral symmetry as outlined above, together with a study of the number and orientation of floral parts, leads to a useful convention, namely, the **floral diagram,** in which these features are depicted on a number of concentric circles representing the various whorls in the flower. The axis of the inflorescence is inserted at the top of the diagram, in its proper *posterior* position, and the bract below stands in the *anterior* position. The diagram may also be used to show fusions between the various members; for example, the petals may be linked up to show a sympetalous corolla, or the stamens may be joined to the corolla to indicate epipetaly, as is shown in some of the diagrams accompanying the illustrations at the end of this book.

Another convention, that of the **floral formula,** indicates, in abbreviated form, the number of members composing the flower. If we use the symbols K for calyx, C for corolla, A for androecium, and G for gynoecium, the composition of the Primrose flower, for instance, may be expressed by

$$K_{(5)}[C_{(5)}A_5]G_{(\underline{5})},$$

in which the brackets indicate gamosepaly, epipetaly, sympetaly, and syncarpy; the line below the number of carpels shows that the gynoecium is superior. Again, the formula for the monocotyledonous flower, say the Daffodil, is

$$[P_{(3+3)}A_{3+3}]G_{(\overline{3})},$$

showing that this flower has a perianth P (not differentiated into K and C) in two whorls, and that the syncarpous gynoecium, from the insertion of the line above the number of carpels, is inferior; the brackets enclosing perianth and stamens imply epiphylly.

When the number of members in a whorl or set exceeds ten, it is the custom to state that the parts are numerous by using the symbol ∞ (e.g. in the *Ranunculaceæ* and *Rosaceæ*, after A and G).

CHAPTER V

Development of the Sporangia; Cytology and Formation of the Sexual Cells

All the cells and nuclei of the plant body (soma) arise from pre-existing ones which are descended, if the plant is sexually produced from the single cell of the fertilized ovum.

Moreover, when cell-division takes place, it is preceded by the division of the cell nucleus, and the two resulting cells are in every respect identical. It is true that in the plant body the descendant cells become differentiated to fulfil the many functions of the body, but the mechanism of cell-division in any part follows the same definite laws whether it operates in root, stem or leaf, and the characters of the nuclei remain unchanged throughout the vegetative life of the plant.

To investigate the cause of this remarkable constancy in the nuclei, we have to examine their minute structure and particularly the sequence of events which takes place when they divide. It is difficult to make out nuclear structure from observations of living cells, and the modern science of cytology has been built up almost entirely around a very efficient technique by which the whole story of nuclear division may be pieced together from microscopic examination of plant tissues which have been killed and " fixed " by immersion in suitable reagents and after diverse processes stained appropriately with various dyes.

A faint idea of the living nucleus can, however, be obtained by microscopic examination of a small quantity of the soft pulp of a fruit such as the Tomato. The cells, isolated from their neighbours, are ovoid in shape, and the nucleus can be seen as a small transparent sphere suspended in the thin cytoplasmic fluid of the cell. Embedded in the clear nucleus is a much smaller and opaque body, the nucleolus, about the formation of which very little appears to be known, and of which no further mention need be made. Even under very high magnification little more can be made of the contents of the nucleus except that it appears to be bounded by a thin membrane enclosing a transparent mass in which, according to some observers, a faint network can sometimes be detected. This is the usual appearance of all nuclei when in a resting condition, that is, when division is not taking place (fig. 25, A).

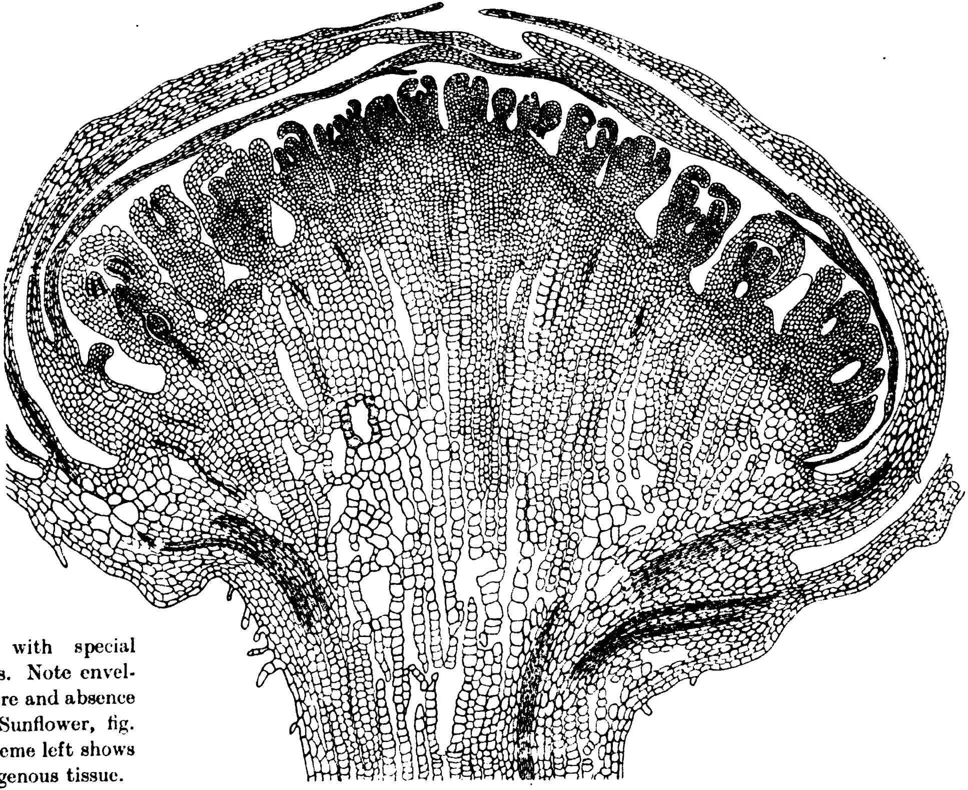

Fig. 20. The Capitulum of *Chrysanthemum*. —Median section. Development of florets with special reference to that of anthers. Note enveloping bracts of the involucre and absence of inter-floral bracts (cf. Sunflower, fig. 10). The floret on the extreme left shows a young anther with sporogenous tissue.

At the approach of cell-division (in preparations suitably fixed and stained) the nuclear contents appear as a tangle of threads like a loosely wound ball of wool. The threads readily take up various kinds of dyes, a process which greatly facilitates the study of nuclei and without which, indeed, it would be impossible to study their behaviour at cell-division. Cytologists are now agreed that the mass of threads is not a single skein intricately wound but consists of a definite number of distinct threads (fig. 25, B). These threads are called **chromosomes** and their number (with rare exceptions) is constant for every species of plant. Thus the Lily has 24, Potato 48, Radish 18, Red Currant 16, Strawberry 14 chromosomes in the nuclei of the vegetative (somatic) cells. A chromosome, again, consists of a definite number of particles called **chromomeres** which appear like so many beads of various sizes arranged at unequal but fixed intervals along the chromosome.

Careful examination reveals an important feature of somatic chromosomes, namely, that they are split along their entire length into two identical halves. Each half-chromosome is known as a **chromatid** (fig. 25, C) and each half receives an equal share of every chromomere. The chromosome-split is really a portent of the separation of the chromatids at the next division of the nucleus, but before this takes place, each pair of chromatids undergoes considerable contraction in length. These early stages of nuclear division, known as the **prophase,** are succeeded by the **metaphase,** at which the greatly condensed chromosomes (it is now difficult to recognize their split condition) after disappearance of the nuclear membrane, arrange themselves in the form of a plate across the middle of the cell. For their accommodation in this position there arises in the cytoplasm what appears to be a system of fibrils shaped like a spindle, the middle part forming the " equator " and the two apices the opposite " poles " of the so-called nuclear spindle. It is on the equator that the contracted chromosomes at the metaphase stage (fig. 25, D, E) arrange themselves in plate fashion. For their retention in this zone each is furnished with a **centromere,** which appears like a constriction in the chromosome, but is really a very small part of fixed location which does not absorb the dye in the same way as the rest of the chromosome. Each chromosome appears to adhere to the spindle by its centromere. The chromosome-split again becomes manifest and the half-chromosomes are seen to separate from each other—the **anaphase** stage (fig. 25, F, G)—as if by mutual repulsion. The chromatids derived from the same chromosome travel to opposite poles of the spindle. Having arrived at the poles—the **telophase** stage (fig. 25, H)—the chromatids may further contract, and the two sets gradually assume the character of typical nuclei; meanwhile, the half-chromosomes attain the size of full chromosomes (fig. 25, J). Finally, a cellulose wall in the plane of

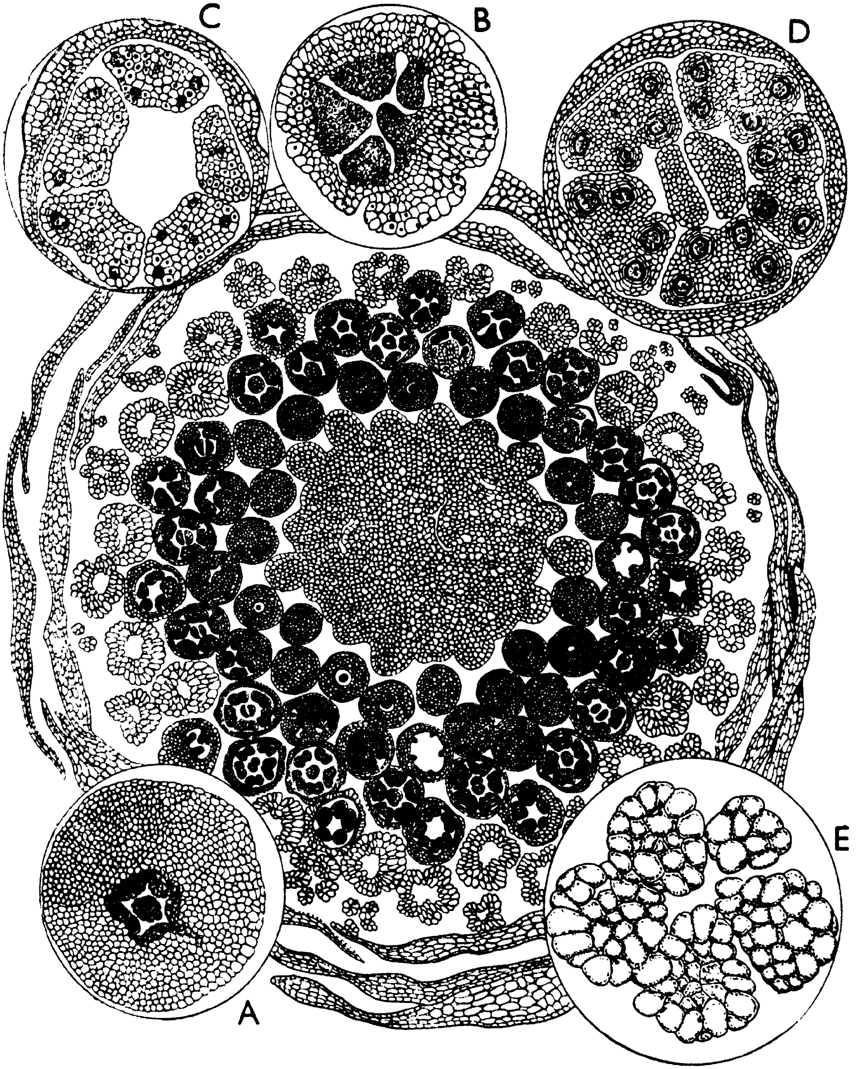

Fig. 21. The Capitulum of *Chrysanthemum*.—Transverse section, at an older stage than that in fig. 20. The central tissue is the capitulum axis. Many stages of anther development can be traced from the central primordia to the outer florets. A the five anther primordia (dark shaded) around a shallow depression at the base of which is the apical meristem of the floret (only the central part shown). B a later stage. C the five anthers cut across above the level of their union with the corolla; note four-lobed appearance and differentiation of the dark-shaded hypodermal cells. D later stage showing early formation of sporogenous tissue; bifid style at the centre. E lobes of corolla.

the equator is built across the cell, isolating the new nuclei, and thus two cells of identical nuclear structure are formed (fig. 25, K). This briefly is the history of nuclear division as it occurs in any part of the vegetative plant. The process is called **mitosis** or the **mitotic division**; it is an orderly procedure by which the characters of the nuclei are permanently maintained throughout the vegetative history of the plant.

After a period of vegetative activity the plant usually resorts to sexual reproduction. As this phenomenon in the history of the flowering plant ends in the formation of seeds, the development of the plant organs, the anther and ovule, which are directly responsible for seed-formation will now be described, and the inquiry must also include the mode of formation of the reproductive cells within these organs, with special reference to the history of their chromosomes.

(i) The Pollen-sacs (*Microsporangia*) and Pollen Grains (*Microspores*)

Early stages in the development of the anther are looked for in very young flower buds, for the anthers are usually developed greatly in advance of the carpels. In most floral types the details of anther development are very uniform, and the cases taken here for illustration, namely, the Sunflower (figs. 10, A, K, and 22) and the Chrysanthemum (figs. 20 and 21), are selected because their young capitulum inflorescences (examined in both transverse and longitudinal sections) show a continuous series of stages of anther development starting near the centre of the inflorescence, where very young florets are found, and continuing towards the margin, in radial direction, to the older florets. Fig. 22 shows the five anther-primordia of a young floret of Sunflower in transverse section; a four-lobed condition is early apparent in each of the primordia. Four vertical rows of cells, one row in each lobe, situated immediately beneath the epidermis, soon become prominent by virtue of their size, large nuclei and density of cytoplasm. These vertical rows of **hypodermal** cells, which extend the whole length of the young anther, initiate the formation of the four pollen-sacs (microsporangia) and their contents, the pollen grains (microspores).

The tissue at the centre of the anther primordium is called **connective tissue,** and here a vascular strand soon becomes differentiated. This strand forms the vascular supply which passes up through the anther-stalk or filament; the latter, however, is not fully extended until just before the opening of the flower. The four anther-lobes follow identical lines of growth and therefore it will suffice to describe the changes in one of the four rows of hypodermal cells. In some

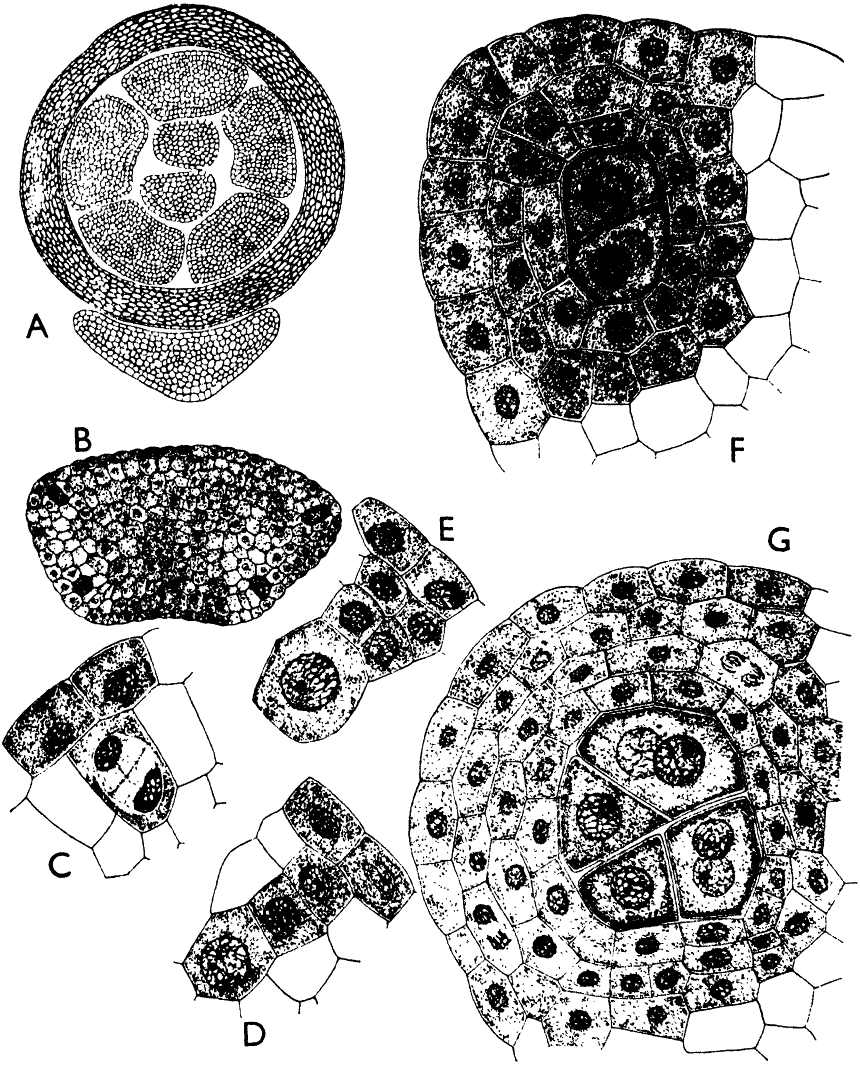

Fig. 22. Development of the Anther.—A, transverse section of a floret of Sunflower (fig. 10) showing undifferentiated primordia of the five anthers, surrounded by corolla, with anterior bract below. B further details of one anther, showing the four hypodermal cells with dark contents. C hypodermal cell in mitosis. D hypodermal cell dividing tangentially to form two parietal cells and an inner larger sporogenous cell. E radial divisions in parietal cells. F division in sporogenous cell and further radial divisions in surrounding parietal and epidermal cells to form anther lobe. G, additional parietal layer surrounding large-celled sporogenous tissue is the tapetum. The sporogenous tissue is now surrounded by three parietal layers with epidermis outside.

cases, however, anthers may have only two pollen-sacs, traceable in origin to two such rows; it may also occur that one or more of the hypodermal rows becomes abortive, as sometimes happens in abnormal anthers of the Chickweed (*Stellaria media*); in other types again, as in the anthers of the Potato flower, each sac originates from a group of hypodermal cells. These cases, however, are exceptional.

Normally, each hypodermal cell of a row becomes divided unequally by a wall parallel to the surface; the inner, larger cell is called the **sporogenous** cell or **archesporium,** the smaller outer one, the **parietal** cell. By further tangential divisions the latter forms two or more, usually three, layers, of which the innermost abutting on the sporogenous cell is known as the **tapetum** or tapetal layer, the others outside it being still called parietal cells. Meanwhile the sporogenous cell is preparing to divide, but as the products of its divisions are not arranged in layers, as are those of the parietal cells, but form instead a central group, the epidermal and parietal cells including the tapetum, in order to keep pace with the increase of sporogenous cells, divide rapidly in radial fashion, that is, by walls at right angles to the surface of the anther lobe. Consequent upon the radial and tangential divisions of these cells, the sporogenous tissue becomes almost completely invested by the layers of parietal cells. The latter finally present a concentric appearance, which is more pronounced around the outer contour of the anther lobe than towards its inner limits abutting on the connective tissue. The sporogenous tissue is, however, completely invested by the tapetal layer.

The anther primordium not only expands laterally at its four lobes, but also grows forward and gradually assumes the four-grooved cylindrical form of the typical anther. Cell divisions contributing to the increase both of sporogenous and to a limited extent of parietal tissue accordingly take place in three dimensions, so that the pollen-sacs eventually extend along the whole length of the anther.

When the sporogenous tissue is well established, its cells, now called the **spore mother-cells,** are seen to be in close contact at all points and filled with densely granular cytoplasm in which the nuclei are very prominent. All cell divisions within the anther up to the formation of the spore mother-cells are mitotic, that is, they are ordinary nuclear divisions with the same number of chromosomes as in other cells of the plant body. But as the mother-cells are now about to enter upon the formation of pollen grains (which eventually form sexual cells) it follows that should fertilization take place between male and female cells containing the same number of chromosomes as in the mother-cells, the embryo would come to possess twice the number found in the parent plant. (In some species this does actually occur, but rarely.) The number of chromosomes is, however, constant for every species

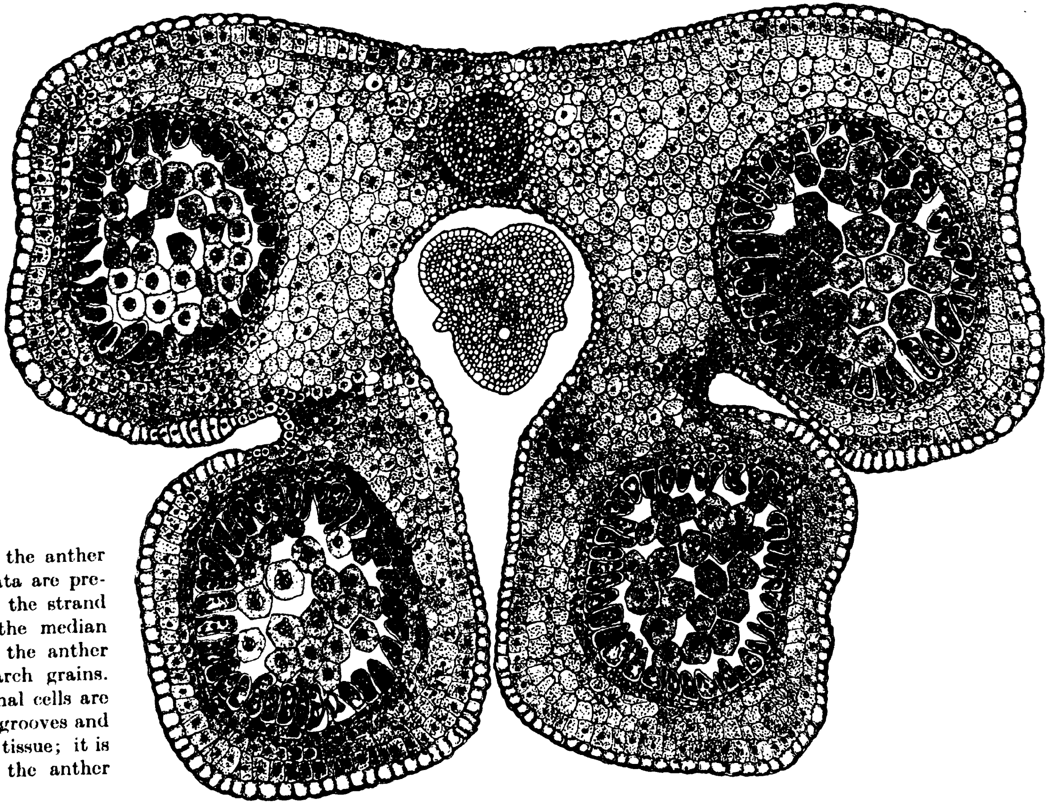

Fig. 23. Anther of *Lilium*. —Transverse section. The two top lobes face the exterior of the flower and overarch the two inner lower lobes. The sporogenous tissue has formed spore mother-cells which are separating from one another owing to the general expansion of the anther tissues; most of the mother-cells are about to enter upon the "reduction phase" (meiosis); they are surrounded by the dark-stained, wedge-shaped cells of the tapetum. Note prominence of hypodermal layer at all points except in the deep median groove where the filament of the stamen has been cut across. In the connective region of the anther is a vascular strand. Stomata are present in the epidermis above the strand as well as in that lining the median groove. All the tissues of the anther lobes are very rich in starch grains. Note that typical hypodermal cells are absent from the two lateral grooves and are replaced by small-celled tissue; it is at these two regions that the anther will dehisce.

(with rare exceptions) and in order to prevent a doubling of the chromosome-complement in the union of male and female nuclei, a **reduction phase** whereby the number of chromosomes is reduced to half must take place at some point during the formation of the sexual cells. Such a reduction, known as **meiosis**, actually occurs when every spore mother-cell gives rise to four pollen grains. The process is also referred to as the **tetrad** division; a similar reduction phase also takes place in the ovules. Accordingly, every pollen grain normally receives a half-set of chromosomes, and on account of this, the pollen grain is referred to as **haploid**, that is, bearing half the number, or *n* chromosomes, the parent plant being called **diploid**, possessing 2*n*, the full number of chromosomes.

Meiotic nuclear division occurs in all plants sexually produced and is a provision in the life-cycle whereby the number of chromosomes in the nuclei of the sexual cells, male and female, may be half that in the vegetative nuclei. This critical division is really of far greater import than mere reduction in the chromosome complement of a species, and it is now generally agreed that it operates the mechanism which not only is responsible for the transmission of hereditary characters from parent to progeny, but may also account for the appearance of " variations " (Chap. XI) in descendant plants.

To resume the history of the spore mother-cells it is convenient at this point to study their further development in the anther of the Lily (*Lilium*) (fig. 23), this type being well known for the clarity of the nuclear phases. The tapetal cells surrounding the sporogenous tissue are seen to be rich in contents and many of them are furnished with more than one nucleus. A remarkable feature presented by the remaining tissues of the anther, connective as well as parietal, is their richness in starch, and this is particularly evident in the hypodermal layer. The young anther is thus well laden with food reserves. As a result of the general expansion of the anther by growth, the spore mother-cells gradually tend to separate from one another, at first appearing somewhat angular in outline but later becoming spherical when quite free from one another. At this time, too, a significant change is taking place in the tapetal layer, for its cells are showing signs of disintegration. During this process they become radially elongated, appearing as so many wedge-shaped cells with their pointed ends directed towards the spore mother-cells. It is no doubt the function of the tapetum to nourish these cells, for the progressive development of the latter is attended by shrinkage of the tapetal layer. The separation of the mother-cells from one another enables them to assimilate through their thin walls far more readily than if they remained in close contact, for they are practically bathed in the nutritive material derived from the tapetum (fig. 24).

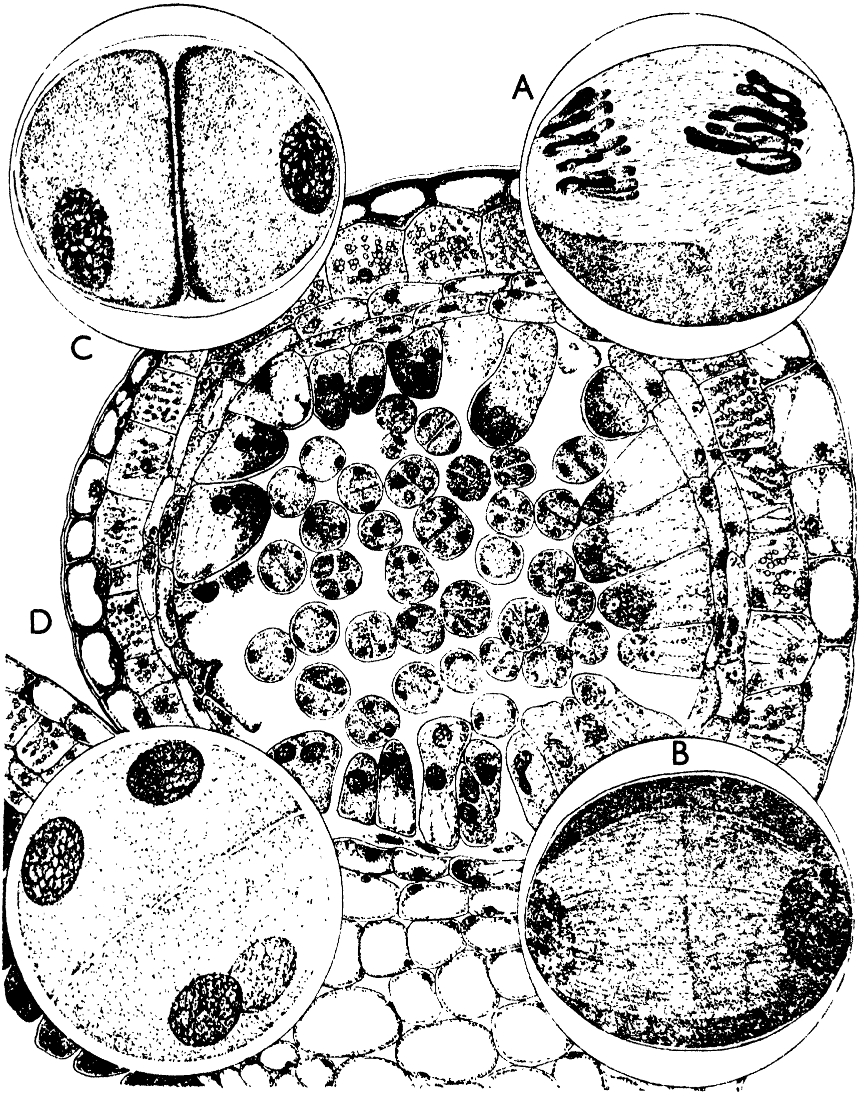

Fig. 24. Anther Lobe of *Lilium* showing Tetrad Formation.—Transverse section. Spore mother-cells in various stages in the formation of tetrads, surrounded by disintegrating, wedge-shaped tapetal cells, some of which are multinucleate; the hypodermal cells are prominent and with the progressive disappearance of their starch contents, fibrous thickenings are laid down on all their internal walls except the outer. Inset: A, spore mother-cell showing thick staple-shaped chromosomes, at *anaphase*; note constriction of the cytoplasm at top. B the two nuclei at the *telophase* stage, separated by " spindle fibres "; note early appearance of equatorial cleavage in the cytoplasm. C two-celled condition of spore mother-cell with cleavage complete. D four-nucleate condition before second cleavage to complete the tetrad.

Illustrations of the various phases of **reduction** are given in fig. 25, L to U, where a hypothetical case is taken of the nucleus of a spore mother-cell furnished with twelve chromosomes as its diploid number. The figures are based on observations of divisions in the anthers of a species of Lilium, in which actually there are more chromosomes, here omitted for clearness. The earliest (**leptotene**) stage in meiosis shows the chromosomes to be evenly distributed (fig. 25, L) within the nucleus, but there is no evidence, at this stage, that they are split longitudinally as in mitosis. At the onset of nuclear division, as was previously mentioned in the account of mitosis (p. 56), high magnification shows a chromosome to consist of a definite number of particles called **chromomeres** which appear like beads of various sizes arranged at unequal intervals along the chromosome. We have also noted that the number of chromosomes in the nuclei of a given plant is constant, and numerous investigators have further established the facts that individual chromosomes, in many species, can be distinguished from the rest not only by characteristic differences in size but also by the relative spacing of their beaded particles. Great stress is accordingly placed on the constancy of chromosome features, both quantitatively and qualitatively, for it is realized that when nuclear division takes place the longitudinal splitting of the chromo-

Fig. 25. A to K, *Mitosis*; L to U, *Meiosis*. Diagrammatic.—The two divisions show the behaviour of 12 chromosomes which, for clearness, are shown in one plane of focus.

Mitosis: A, B, C, *Prophase* stages. A very early *Prophase*, resting nucleus showing a network appearance, with nucleolus. B 12 chromosomes evenly distributed within nuclear membrane. C 12 chromosomes showing split into half-chromosomes or chromatids. D polar view of split chromosomes at *Metaphase*; note disappearance of nucleolus. E *Metaphase* spindle, with chromosomes forming equatorial plate; note disappearance of nuclear membrane. F separation of chromatids at *Early Anaphase*. G *Anaphase* stage; note formation of new cross-wall. H *Telophase* stage. J organized nuclei after telophase. K final two-celled condition, showing nuclei passing into *resting stage*, as in A.

Meiosis: L, M, N, O, P, *Prophase* stages. L *Leptotene* stage, 12 chromosomes evenly distributed within nucleus; note the "beads" (chromomeres). M *Zygotene* stage, pairing into 6. N *Pachytene*, the coiling stage, and *Early Diplotene* showing splitting of coiling chromosomes, each pair forming four chromatids. O *Late Diplotene*, almost complete absorption of split condition accompanied by looping and general contraction of double chromosomes or bivalents; nucleolus almost completely obliterated. P *Diakinesis*, stage of maximum contraction of the 6 bivalents, which assume various but characteristic shapes; the constricted part in each bivalent is occupied by a hyaline portion, the centromere; complete disappearance of nucleolus. Q *Heterotype Metaphase*, the 6 bivalents at equator of spindle to which they are attached by their centromeres; the latter may now be separated as at q, q'. R *Heterotype Anaphase*, the 6 monovalents travelling to opposite poles; note cytoplasmic constriction; r the two monovalents showing centromeres. S *Heterotype Telophase*, showing close aggregation of thick chromosomes. T *Homotype Anaphase*, showing the two nuclei of previous telophase dividing in mitosis; note t_1 showing half-chromosomes united at their common centromere, and distal parts of the chromatids widely divergent; t_2' chromatids at anaphase. U the four nuclei of a tetrad, each nucleus now organized with 6 fully developed chromosomes; the nuclei become those of the four pollen grains.

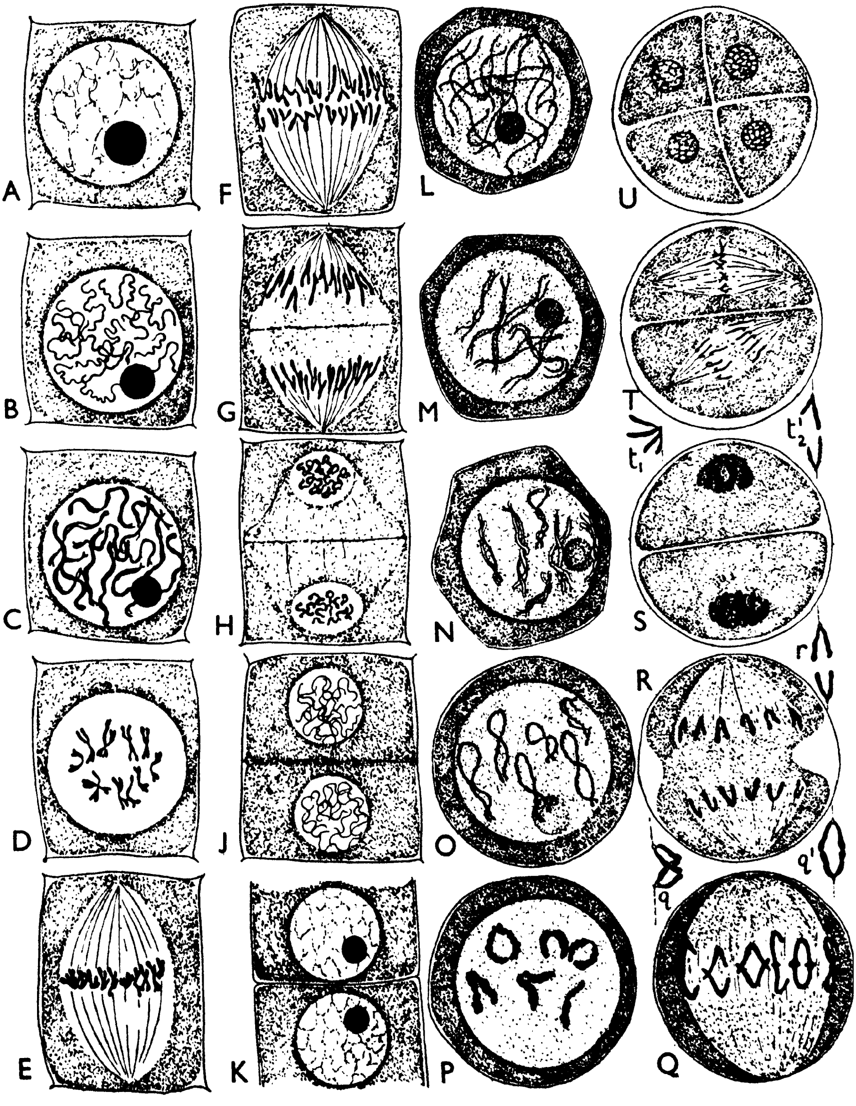

Fig. 25. (For description, see opposite)

somes into chromatids implies an exact sharing of the material of every particle (chromomere) along the thread. In this way complete identity of the nuclei is preserved at every cell division.

After the early stage of **leptotene**, the 12 chromosomes arrange themselves in 6 pairs. The process of pairing does not occur in a haphazard manner; it takes place between like or homologous chromosomes only. The members of a pair are, in fact, paternal and maternal, descended by division from the nucleus of the fertilized ovum to which each parent contributed an equal number of chromosomes. Each of the six chromosomes on the paternal side has its own characteristic features, each has its counterpart on the maternal side, and it is only between such similar chromosomes that pairing is effective.

The phenomenon of pairing, therefore, consists in the chromosomes becoming associated in appropriate or homologous pairs, during which process they lie more or less parallel with each other—the **zygotene** condition (fig. 25, M). This is soon followed by the members of a pair coiling round one another—the **pachytene** stage (fig. 25, N). Emerging from the pachytene condition, the individual chromosomes of a pair now reveal a longitudinal splitting into chromatids (as in mitosis) so that there are now *four half-chromosomes* in close arrangement. This stage, called **early diplotene** (fig. 25, N), is brief, and when the chromatids seek to separate from each other, as if by mutual repulsion, they are now found to be somewhat entangled together, a condition which is said to be due to an exchange of parts between two of the four chromatids. It is not clear how or at what exact stage such an exchange arises, but it is possible that transverse breakage occurs among two of the chromatids, one from each of a chromosome pair. This exchange appears to be effected during the phases when the chromatids are packed together as would be the case at the close of the pachytene stage, where possibly an opportunity would be afforded for the broken portions of two different chromatids to join end to end, thus forming new chromatids from segments of the original ones. This phenomenon is known as **crossing-over** and its visible consequence as a **chiasma,** from the cross-like appearance of the exchange. The processes of crossing-over and chiasmata formation are, however, too complicated to describe in detail in a work of this nature, and therefore only the outstanding features have been mentioned here (see p. 122).

In fig. 26 the chromosomes of a homologous pair are shown, one white and one black; the constriction in each represents the centromere. Directly opposite to the term " prophase " in this figure are the four chromatids, between two of which breakage and segmental exchange have taken place. Of the four chromatids, therefore, two are like the parental types, one " white " and one " black ", and two, which are now reconstituted chromatids, are " part white " and " part

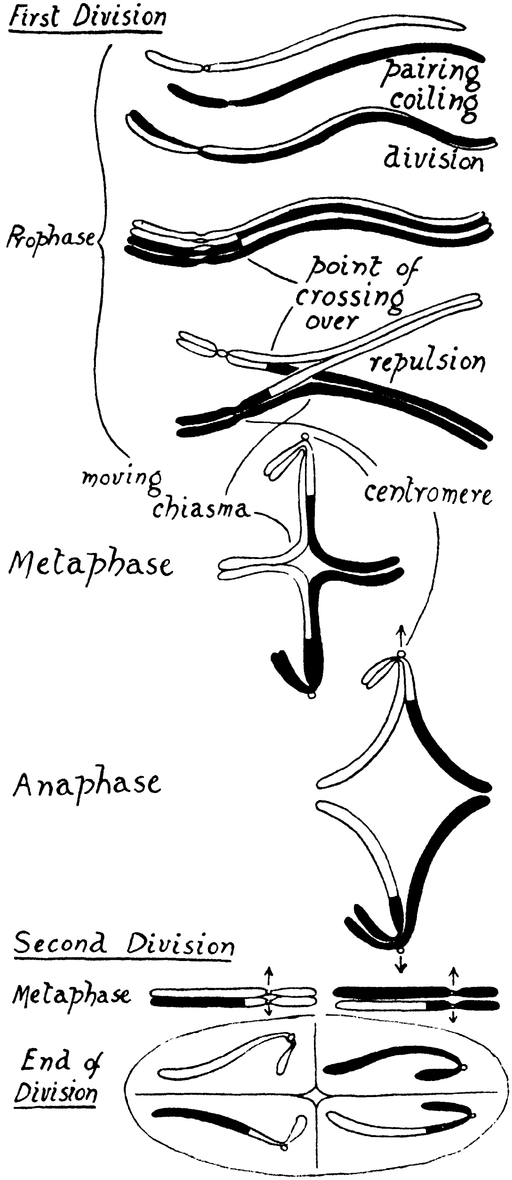

Fig. 26. Diagram showing history of two homologous chromosomes at meiosis according to the chiasmatype hypothesis. Note: the four daughter nuclei all contain chromosomes of different origin owing to crossing-over. By kind permission of Dr. C. D. Darlington (*Recent Advances in Cytology.* 2nd Edition. J. & A. Churchill, 1937).

black ", that is, they share the parental factors. All four chromatids eventually grow to the size of full chromosomes.

When the succeeding stage is complete—**late diplotene** (fig. 25, O)—there may be no signs at all of the four-fold nature of a chromosome pair, for they contract and become variously looped, but stand out very clearly and evenly distributed within the nucleus. The next stage, called **diakinesis,** is marked by maximum contraction in the size of the chromosomes, during which they are spaced evenly apart in the nucleus. Diakinesis is a well-marked feature of meiosis, and the experienced cytologist can frequently distinguish, at this stage, all the different types of chromosomes composing the nucleus. In this he is aided by their characteristic and distinctive shape and also by the position of the centromeres in the double-chromosomes, or **bivalents,** as they are now called (fig. 25, P).

With the approach of the succeeding stage, that of **first metaphase** (fig. 25, Q), the nuclear membrane and the nucleolus disappear, and, as in mitosis, a spindle becomes established in the cell. The bivalents now move into the equatorial plane with their centromeres within the axis of the spindle. It is not clearly known how the centromeres attach themselves to the spindle, but whatever the actual mechanism may be, each double chromosome now separates into two.

As soon as the separated chromosomes are on their way to opposite poles of the spindle, the latter becomes constricted in the plane of the equator, appearing like an hour-glass, and by progressive constriction a plane of cleavage arises in the cytoplasm, whereby the contents are equally divided. During this migratory stage—the **anaphase** (fig. 25, R)—it is important to note that the separating members of a bivalent are *full chromosomes.*

At the **metaphase,** the bivalents are arranged at random on the spindle and it is a matter of chance which chromosome of a pair travels to one pole or the other. When the chromosomes are at their respective poles, at the **telophase** stage (fig. 25, S) the critical stage is reached where the daughter nuclei possess half the total number of chromosomes, in the hypothetical example, six in place of twelve. Hence the term " heterotype " for this, the first part of the reduction phase. Usually without a period of rest, the two newly constituted nuclei enter upon the second division, which is a mitotic one, hence called the " homotype " division. For this division each daughter cell will divide in the usual way (fig. 25, T). Thus when the two divisions are complete, four cells are produced, each containing the reduced number of chromosomes, namely six.

Although there are many similarities between the two types of nuclear division, mitosis and meiosis, one important feature stands out in the latter, namely, that the chromosomes of different parentage,

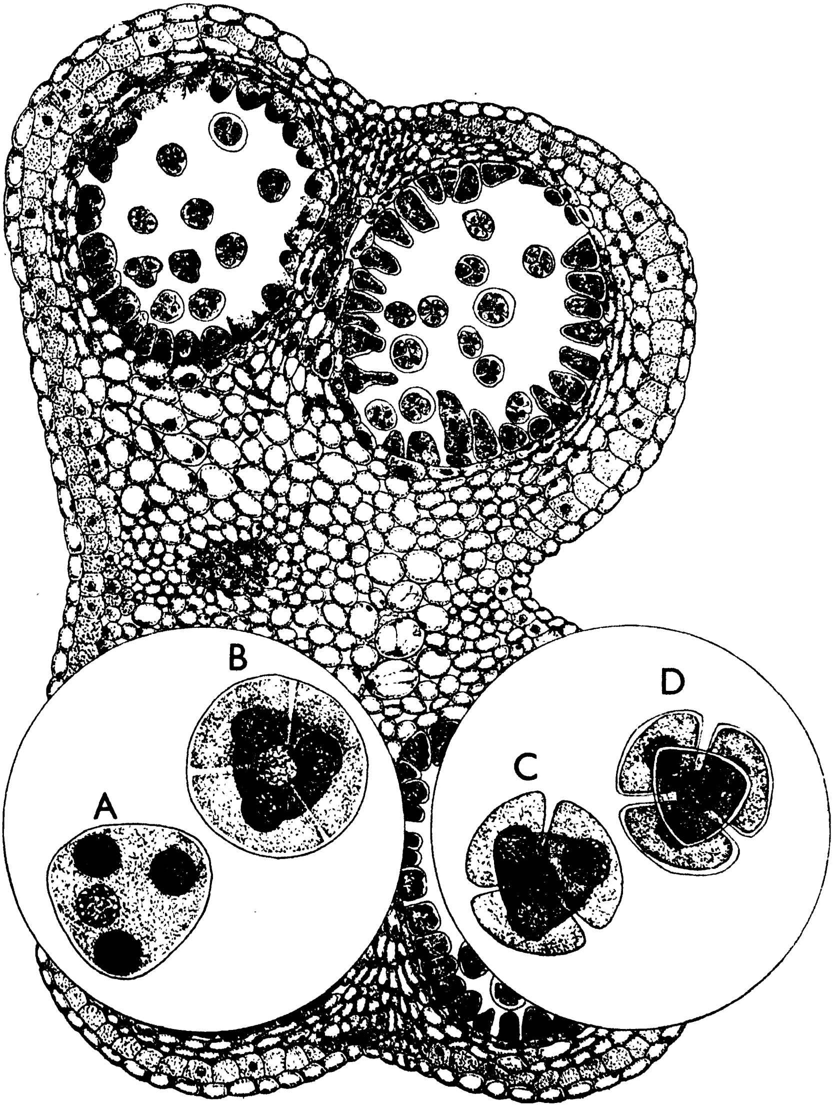

Fig. 27. *Caltha*.—Transverse section of Anther showing Tetrads. Note that here, and in Dicotyledons generally, all four nuclei forming a pollen tetrad are organized, as shown in A, before cleavage of the cytoplasm begins. B cleavage around each nucleus takes place in tetrahedral fashion; each pollen grain will have three inner flat surfaces and an outer curved surface. C disappearance of wall of pollen mother-cell; tetrahedral arrangement of released pollen grains; D each grain has formed its own double wall, the intine and extine.

by virtue of crossing-over, are given an opportunity to become *exchanged for a part or parts of their length.* When the chromosomes finally enter the four cells or pollen-tetrad, if we adopt the convention of " black " and " white " for the homologous chromosomes, as in fig. 26, one pollen grain will have a " white " chromosome; one a " black " chromosome; and two will each have a chromosome " part-white " and " part-black ".

At the end of the heterotype phase, the two daughter nuclei are separated by a complete cleavage of the cytoplasm in the plane of the spindle equator (fig. 25, S). The second division, the homotype, takes place in each daughter cell, and when another plane of cleavage arises nearly at right angles to the first, four nucleated portions are formed, which are destined to become the four cells of the pollen-tetrad (fig. 25, U). Each portion of the tetrad now secretes a thick outer and a thin inner wall, the **exine** and **intine** respectively. The exine may be smooth, spinous, tuberculated or variously sculptured; it is not equally thick at all parts, and small circular pits, the " germ-pores ", are left at a few places as unthickened areas. (It is by one of these pores that the inner wall emerges to form a pollen tube, at fertilization.)

With the disappearance of the wall of the mother-cell, the four pollen grains are fully organized. In some floral types (e.g. the family *Juncaceæ*, p. 235) the four grains may remain together, more or less in tetrads, up to the time of pollen dispersal, but in most cases they separate freely from one another before anther dehiscence takes place.

The above details of pollen formation and arrangement of the pollen grains in the tetrad are characteristic of Monocotyledons generally; here, as in *Lilium*, the tetrad condition arises as the result of the segmentation of the mother-cell contents by two planes of cleavage at *right angles* to each other. In Dicotyledons, however, as shown in *Caltha* (fig. 27) there are minor points of difference. When the mother-cell divides, the two nuclei formed are not separated by a cleavage of the cytoplasm, as in the Monocotyledon, and not until all four nuclei are organized does the cytoplasm of the mother-cell divide equally into four portions. The method of cleavage is somewhat different and takes place in a *tetrahedral* manner. Each nucleated portion, as in the Monocotyledon, becomes delimited from the others by the formation of an exine as described above.

While the pollen grains are developing, changes are also in progress in other parts of the anther. The tapetal layer gradually becomes improverished of its contents, but it remains almost to the end as a crushed and disorganized layer lining the pollen-sac. During the maturation of the mother-cells, the tissues of the anther wall are very rich in starch, but this substance now gradually disappears as the pollen grains ripen. With the exception of the epidermis and the

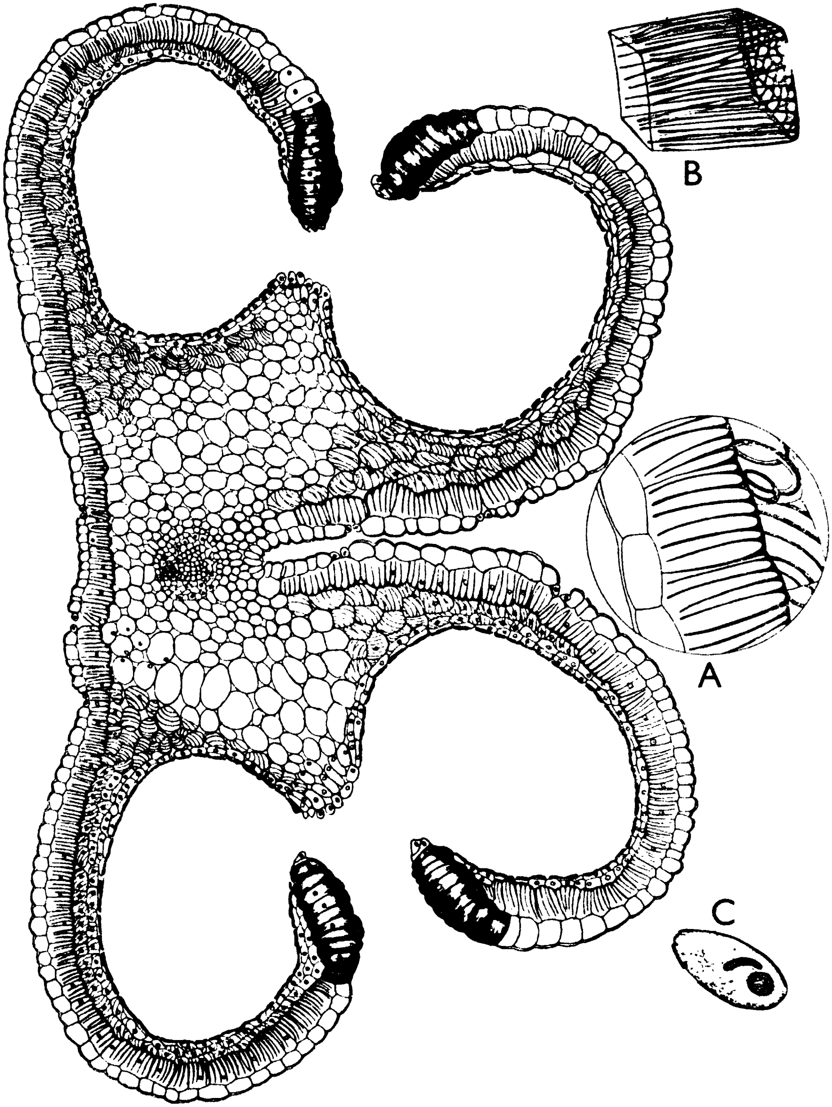

Fig. 28. *Lilium.*—Transverse section of Mature Anther.—Anther after complete discharge of pollen. Cf. fig. 23 and note fibrous thickenings in hypodermal layer and cells adjacent. Note mode of dehiscence at the two lateral grooves where the enlarged epidermal cells have been heavily cutinized; rupture of the tissues between the pollen sacs causes the pollen to be discharged into the lateral fissures. A, portion of hypodermal and sub-hypodermal layers with fibrous thickenings on inner and radial walls. B hypodermal cell with fibrous thickenings on all walls except the one abutting on the epidermis. C pollen grain; germ-pores in the exine; " tube " nucleus round, " generative " (or antheridial) nucleus curved and narrow.

central tissues at the connective region, together with a few cells situated at the lateral grooves of the anther, practically all the cells surrounding the pollen-sacs develop fibrous thickenings on their inner walls. The fibres are, however, far more prominent in the hypodermal layer than in the inner cells, so that this layer in the ripe anther is known as the **fibrous layer** (figs. 24, 28). With the progressive disappearance of the starch in these cells the fibres become more and more evident. Within the hypodermal cells they are laid down on all the internal walls, with the exception of the outer walls abutting on the epidermis. On the inner tangential walls of these cells the fibres form an intricate network, but on the radial walls they remain as simple strands which may, however, frequently branch and anastomose. Where the fibrous thickenings occur in the deeper-seated parenchyma of the connective tissue they may form spirals and loops, again with various anastomoses. The development of the fibrous strands is really a provision for effecting the dehiscence of the anther.

When the anther is ripe for dehiscence the epidermal cells undergo loss of water by evaporation, and in turn draw upon the water in the hypodermal fibrous layer. As a result of the loss of water, the fibrous cells undergo considerable shrinkage and their outer walls, which are not furnished with strengthening fibres, are sucked inwards. The cohesion of the contents within these cells and their adhesion to the walls are so great, however, that the radial walls with their fibrous thickenings are drawn towards each other under considerable strain. Cohesion of the contents at first prevents access of air into the cells, but with continued evaporation, attended by increased shrinkage, the cohesion is finally broken down by the strain. As all the hypodermal and adjacent tissues are under strain, the pollen-sacs are forced to split open at their weakest part, that is, along the two lateral grooves, from which, as was pointed out, the fibrous thickenings are absent. The rupture of the anther walls is therefore localized, but it also extends a little inwards so that the two pollen-sacs in each lobe are

Fig. 29. Ovule Development.—The large figure is a transverse section of the ovary of *Lilium*; the embryo-sacs in the ovules are mostly at the stage shown in D. A, very young carpel of *Caltha* cut across, showing formation of anatropous ovule at marginal placenta. B same in detail, showing single hypodermal cell with dark contents; note beginning of inner and outer integuments and funiculus on the left. C young ovule of *Lilium* showing enlarged hypodermal cell which becomes the embryo sac directly; note inner and outer integuments and suppression of outer integument on funicular side (left). D ovule of *Lilium*, later stage, showing the four-nucleate condition of the embryo-sac; further growth of integuments to form micropyle; nucellus over the embryo-sac reduced to a single layer. E embryo-sac of a *Caltha* ovule (fig. 32) showing complete contents of typical ovule, namely, " egg-apparatus " at top, definitive (endosperm) nucleus at centre, and the three antipodal cells at base; note vacuolated cytoplasm of embryo-sac, which is surrounded by narrow cells of nucellar tissue, equivalent to tapetum layer in the anther.

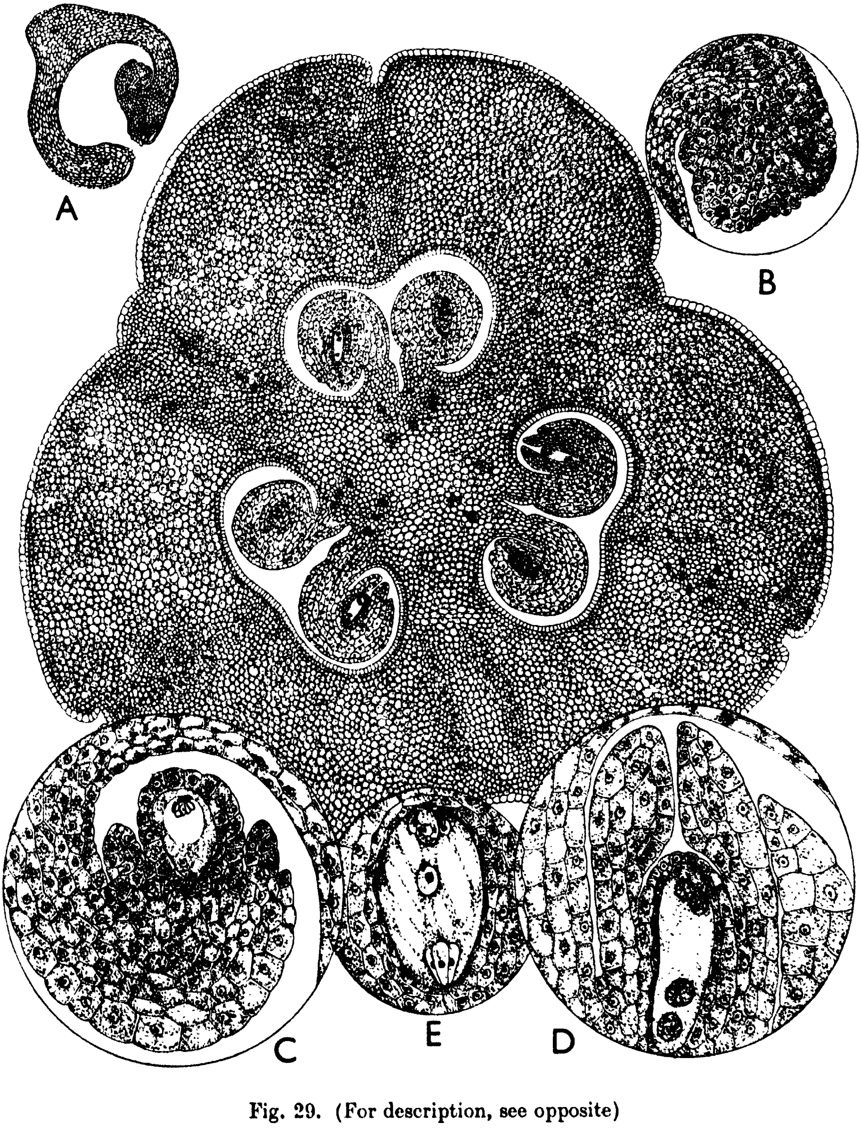

Fig. 29. (For description, see opposite)

finally put into communication with one another. The configuration of the anther lobes decides whether the pollen is to be discharged towards the centre of the flower (introrse dehiscence) or towards the outside (extrorse dehiscence) as in *Lilium* (figs. 23, 28) and *Caltha* (figs. 14, 27) respectively (see p. 29).

The anthers of a flower may not all ripen at the same time; for example, in *Caltha* the innermost of the numerous stamens remain closed, in protection of the carpels, while the outer stamens are widely divergent and dehiscent. In older flowers generally, the anther-fissures gape open to such an extent that their margins curve outwards. These are the usual features of anther dehiscence, but exceptions occur, as for instance, in the flower of the Potato (fig. 56, E), where the pollen is discharged through apical pores, and in the Barberry, in which valves are formed in the anther wall; again, in the Orchis (fig. 70, B), each of the two anther lobes in the single stamen of this flower is represented by a club-shaped structure containing pollen, and one or both clubs may be entirely removed by the visiting insect at pollination. In most flowers, long before they are due to open, the anthers are at an advanced stage of maturity; during this time they are closely packed together in the bud or supported in pendulous fashion on comparatively short filaments, which only attain their full length just before the flower opens (fig. 9).

(ii) The Ovule (*Megasporangium*) and Embryo-sac (*Megaspore*)

The ovule starts its development on the placenta of the carpel as a smooth ovoid protuberance of tissue called the **nucellus** (fig. 29, A). The ovule may have a single or double covering, the **integuments,** beginning as rings of tissue around the base of the ovule. In the case of the double investment the inner integument is laid down first and is followed closely by the outer (fig. 29, B, C). As the nucellar tissue increases, the integuments gradually creep up to invest it, but leave a narrow aperture, the micropyle, uncovered at the top (fig. 29, D). When fully formed the ovule is raised on a slender stalk or funiculus. An ovule may be erect or **orthotropous,** bent or **anatropous,** curved or **campylotropous** (fig. 12, M, N, O) according to the relative positions of the funiculus, micropyle, and chalaza (p. 37). The commonest type of ovule is the anatropous, the development of which will now be described in greater detail.

Important changes in the nucellus set in before the integuments are complete. The case of *Iris* is taken here for illustration as being fairly typical of ovular development generally. As seen in median

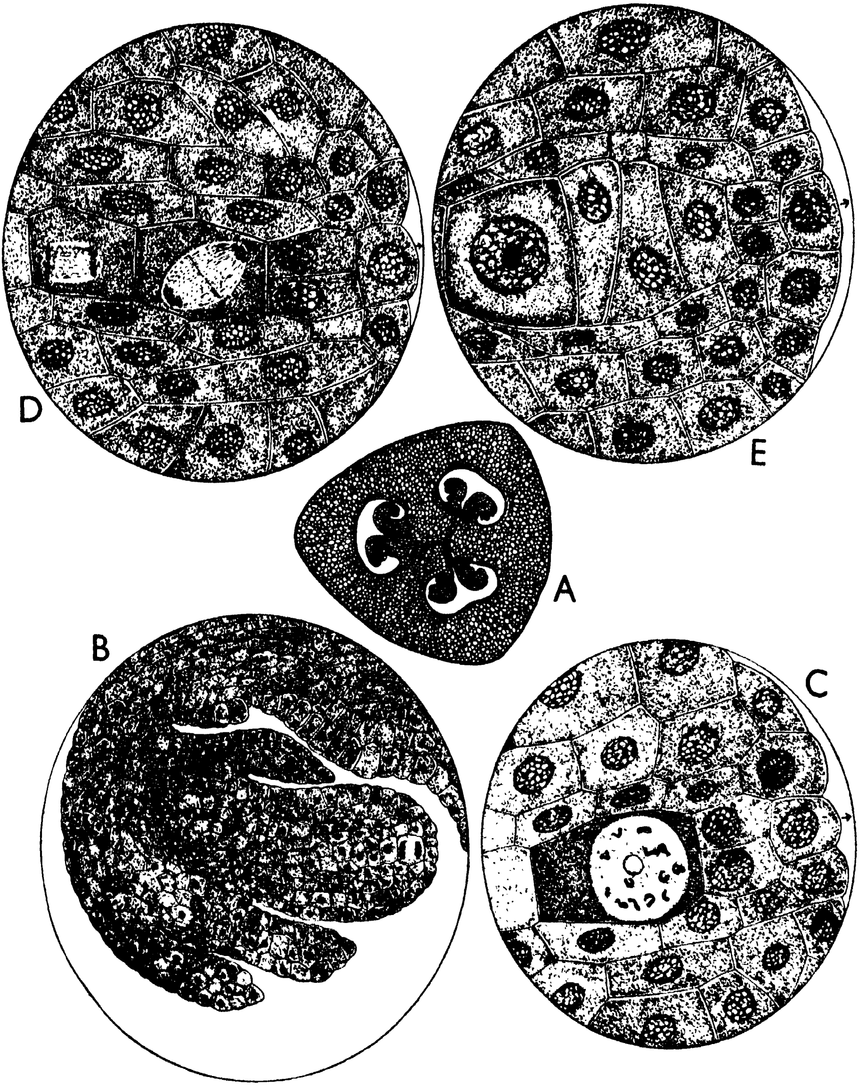

Fig. 30. Ovule Development.—A, trilocular ovary of Iris with young ovules in axile placentation. B young anatropous ovule of Iris, nucellus showing prominent hypodermal cell with its nucleus dividing; note integuments, chalaza, and funiculus. C later stage of nucellar apex showing hypodermal cell having cut off an outer " parietal cell " which is shown here further divided into two by a radial wall; the large inner cell with its nucleus in " diakinesis " is the spore mother-cell. D same, showing divisions to form the linear tetrad shown in E, in which the innermost cell with prominent nucleus becomes the embryo-sac or megaspore. (Small arrows indicate direction of micropyle.)

longitudinal section in fig. 30, B, a single hypodermal cell at the nucellar apex becomes conspicuous as a result of its dense contents and prominent nucleus (in the illustration, shown dividing). The behaviour of this cell is not uniform in all types, but in *Iris* it cuts off a small cell towards the micropyle. This is known as a **parietal cell;** the inner and larger is the **spore mother-cell** (fig. 30, C). In many types of ovular growth, however, the parietal cell is omitted, so that the initial hypodermal cell actually becomes the mother-cell. It may be recalled that the production of parietal cells is the rule in the development of the anther; that the incident sometimes occurs also in the ovule is an interesting case of parallel development during spore formation.

The spore mother-cell now enters upon a tetrad-formation with a **reduction division** comparable to that which each mother-cell in the anther passes through in order to form a pollen tetrad. In the ovule, however, a striking difference is that in general only *one* spore mother-cell is formed (there are exceptions to this). Moreover, the mother-cell divides to form its tetrad differently, in *linear* series in the long axis of the ovule. Furthermore, of the four cells formed, only one of them, the innermost, persists; the remaining cells atrophy (fig. 30, D, E). This single cell becomes the **embryo-sac** or **megaspore.** The nucleus of this important cell is therefore a product of the reduction phase and possesses a **haploid** chromosome complement like that of the pollen grain. It is worthy of note that the megaspore of the Angiosperm is permanently enclosed in the ovule and is a large cell furnished with a single wall. There is accordingly no provision, as in the free pollen grain, for additional protection to the megaspore by the formation of a second wall or exine.

The embryo-sac rapidly enlarges, encroaching considerably upon the surrounding nucellar tissue and assimilating the nutriment stored in it. The cells of the nucellus in contact with the growing megaspore perform a nutritive function similar to that of the cells of the tapetal layer surrounding the pollen-sac.

Development within the embryo-sac is very uniform both in monocotyledons and dicotyledons, and consists of three nuclear divisions, whereby eight nuclei are formed. These are distributed within the enlarged cell in a very constant manner. Three of the nuclei, collectively called the **egg-apparatus,** take up their positions at the end facing the micropyle; the three which constitute the **antipodals** occupy the opposite end, and the remaining two, the **polar** nuclei, are in a central position in the cell (fig. 29, E). Of these nuclei the most important is the middle one of the egg-apparatus, for it is that of the **female cell or ovum**; its two companions, the **synergidæ**, are of minor importance and doubtful function. A deviation from the normal formation of a tetrad is shown in the ovule of *Lilium* (fig. 29, C) where the derivation of the embryo-sac is simpler, for the initial hypodermal cell itself becomes the megaspore and accordingly the reduction phase is involved in the history of its eight nuclei.

This is the condition of the mature ovule ready for fertilization. The embryo-sac, now a cell of considerable dimensions, has absorbed most of the surrounding nucellus, which appears crushed against the walls of the integument. The sac is filled with vacuolated cytoplasm which is somewhat denser towards the wall; the prominent ovum flanked by the synergidæ stands a little way below these; the antipodals at the remote end are furnished with a thin cellulose wall, whilst at the centre the two polar nuclei remain independent or they may have already fused together to form the "**definitive**" nucleus (figs. 29, E; 32).

CHAPTER VI

Pollination

Before fertilization of the ovule can be accomplished pollen grains must be deposited on the stigmatic part of the carpel. The transference of pollen from stamen to stigma is known as **pollination** and is effected through various agencies. The principal agents are wind and insects—the former type of pollination is called **anemophilous,** and the latter **entomophilous.**

It is important to discriminate between two methods of pollination, **self-pollination** and **cross-pollination.** Both are widespread in nature, and when we examine them more closely we find that these processes are indirectly responsible for the creation of different types or **varieties** of plants. In the practice of hybridization the plant breeder resorts to both methods of pollination for the improvement of his plants.

We speak of self-pollination when transference of pollen from anther to stigma takes place in one and the same flower, and we also apply the same term to the conveyance of pollen from one flower to another on the same individual plant—whether this is done through natural agency or by the brush of the plant breeder. Cross-pollination, on the other hand, implies that pollen is conveyed from one individual to another of the same kind or of a closely related kind.

Numerous investigations on the relative merits of self- and cross-pollination establish beyond doubt that in many plants, with few exceptions, better seeds which grow into more vigorous plants are obtained as the result of cross-pollination than of self-pollination. It is of great interest, therefore, to note from a study of floral structure (Part II) the numerous mechanisms which tend to hinder self-pollination and favour cross-pollination. Though these devices are usually very successful in thwarting self-pollination, the latter process is not

Fig. 31. Pollination.—Style of *Œnothera biennis,* Evening Primrose. A, longitudinal section, showing one of the curved stigmas. The dark-shaded tripolar pollen grains are seen attached at various points. B tripolar pollen grain about to produce pollen tube. C pollen tubes traversing stylar tissue. D pollen grain of *Narcissus Jonquilla* germinated in 5 per cent cane sugar; the two sperm nuclei or male gametes are indicated diagrammatically.

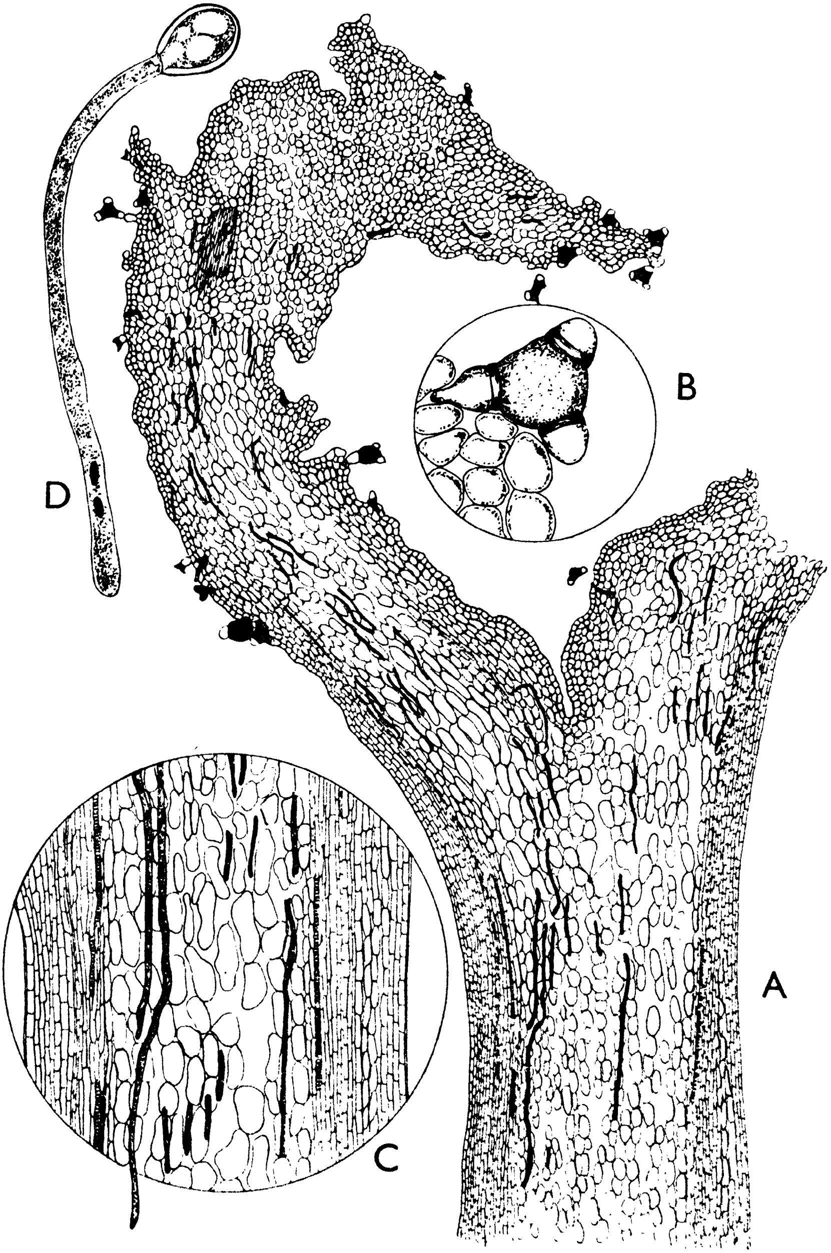

Fig. 31. (For description, see opposite)

entirely excluded, and there are but few flowers which are not able to resort to it in the event of cross-pollination failing to occur.

The length of life of pollen varies considerably in different species, round about a month being an average period, but in many types, e.g. the Grasses, the pollen becomes ineffective after one or two days. A dry sunny day is the best time for pollination; complete soaking has the effect of bursting the grains, but this hardly ever happens, for not only are the minute powdery grains difficult to wet but most flowers are able to protect their pollen in wet weather by partially closing or drooping.

The plant breeder is able to control pollination, but under the unrestricted conditions of nature both methods of pollination obviously take place widely. If under these open conditions one and the same plant produces some seeds which are the products of self-pollination and others of cross-pollination, it is only natural to expect that the offspring from the " crossed " seeds will turn out to be better plants than those from the " selfed " seeds. Of the countless seeds often produced by individual plants, all cannot thrive, for under like conditions of environment competition is severe among plants of like kind, and among them the mortality of the seeds and young plants is very high.

During a long period of flowering, in a garden of mixed flowers, for instance, one would probably find on the stigma of any flower a great assortment of pollen grains obviously brought from flowers of different kinds. The pollen grains of, say, a Rose, Lupin, Delphinium, Wallflower, Viola, &c., are found, under a microscope, to be strikingly different in shape, size, colour and particularly in the character of the wall (exine). Of all the pollen that may be brought to a flower, however, it may be stated as a general rule that only that from the same species of plant or a variety of it is effective for fertilization. Any other pollen on the stigma is *foreign* and soon perishes.

Flowers attract insects by their bright colours and scent. The conveyance of pollen from one flower to another is, of course, purely incidental to the visit of the insect in search of food in the form of nectar or the pollen itself. With few exceptions, entomophilous flowers are furnished with nectaries (honey glands) consisting of specialized tissue secreting a sugary fluid, which the insect exploits immediately it lands on the flower. Some insect-visited flowers, however, are devoid of nectar and furnish the visitor only with pollen, which is borne away to the hive and on which the insect and its larvæ feed.

Nectaries vary a great deal in form in different floral types and their position in the flower appears to be related to the specific manner in which the appropriate insect enters the flower. The so-called " honey-guides " which take the form of lines of darker hue on the corolla are said to be directive to the insect in search of nectar (e.g. Violet). They also occur in the flowers of Broom, Lupin, Gorse, &c., which contain no nectar, but it is possible that in these flowers, which are visited for their pollen, the capacity for making nectar has been lost.

The commonest types of pollinating insects are the ordinary hive bees and humble bees, which appear to be partial to yellow, blue, and purple flowers. Most red flowers and those of lighter hue, white or cream, are visited chiefly at dusk by moths, though butterflies are also seen to visit these flowers during the day. The abundant hairs on the insect's body are instrumental in collecting pollen at the slightest touch of the ripe anther, and should the pollen-laden insect come in contact with a receptive stigma, the adhesiveness of the latter ensures immediate retention of the pollen. There is, however, a factor of greater importance than colour selection in deciding what kind of insect is suitable for pollinating particular types of flowers.

The various species of bees differ in the length of the nectar-sucking organ (*proboscis*), so that a flower with deep-seated nectar would probably not be pollinated by the shorter-tongued bees or flies. Such flowers, e.g. those with long corolla tubes like the Honeysuckle and Convolvulus, are effectively pollinated only by such insects as have a long proboscis. Many flowers with concealed nectar are furnished with barriers of hairs within the corolla tube, as in Dead-nettle (*Lamium*) (fig. 57), whereby small marauding flies are prevented from access to the nectary at the base.

Nectaries may be associated with any of the floral members. In the Barren Strawberry (*Potentilla Fragariastrum*) nectar is secreted by the inner surface of the concave receptacle; in the Lesser Celandine (*Ranunculus Ficaria*) and the Buttercups, the nectary is situated in a small pocket situated at the base of each petal (fig. 1); in the Monkshood (*Aconitum Napellus*) two of the petals are modified into claw-shaped structures wherein nectar is secreted (fig. 40); the Christmas Rose (*Helleborus niger*) has also a number of petal-like nectaries which are shaped like small flasks. There are also various types of petals which are prolonged into narrow tubular spurs, as in the Toadflax (*Linaria vulgaris*), Columbine (*Aquilegia vulgaris*), Orchis (*Orchis*) (fig. 69), &c.; these " spurred " flowers usually have no actual nectar, but the insect extracts the sweet sap by puncturing the lining of the spur.

Nectaries associated with stamens are found in the Violet (*Viola*) (fig. 42, E), where the " connectives " from two of the five stamens are prolonged into two tails or appendages which pass into the spur of the anterior petal; vestiges of honey glands are also found on the staminal filaments of the Traveller's Joy (*Clematis Vitalba*) (fig. 38, H); in the Wallflower (*Cheiranthus Cheiri*) (fig. 41, D) greenish nectary glands are situated at the base of the two lateral stamens. Nectaries are also found in association with the gynœcium. In the Marsh Marigold (*Caltha palustris*) they take the form of glandular epidermal hairs at the sides of the carpels (fig. 32); in the flowers of the *Umbelliferæ*, the nectar is exposed on the epigynous disc immediately above the carpels (fig. 54, E). In many tubular flowers the nectary is commonly a ring or scale at the base of the ovary, as in the Foxglove (*Digitalis purpurea*) (fig. 58) and the Dead-nettle (*Lamium album*) (fig. 57) respectively. In some epigynous types of flowers, as in the Daffodil (*Narcissus Pseudo-narcissus*) or its relative, the Jonquil (*Narcissus Jonquilla*) (fig. 67), there are small pockets at the apex of the ovary immediately above the carpellary septa, which exude nectar into the base of the perianth tube; in the Iris (*Iris Pseudacorus*) (fig. 68, F) there are three pairs of glandular papillæ at the base of the stylar and perianth lobes.

A study of the many devices which appear to be favourable to cross-pollination seems to indicate a direct relation between the mechanisms concerned and the positions of the nectaries. Some of these mechanisms are discussed in connexion with the floral types at the end of this book.

In addition to the structural devices in flowers which appear to hinder self-pollination, there is frequently the condition of **dichogamy,** which means that the discharge of pollen and the receptiveness of the stigma in the same flower do not occur at the same time. Indeed, in flowers of simple structure like those of the Buttercup family, dichogamy appears to be the only means (often unsuccessful) of averting the deposit of self-pollen. When the stamens are discharging their pollen before the stigmas of the same flower are receptive, the condition is known as **protandry.** This is far more common than the reverse state of **protogyny,** where the stigmas are ripe before the anthers are open.

In the flowers of most members of the *Ranunculaceæ* (figs. 38 to 40) the outermost of the numerous stamens shed their pollen outwards, whilst the inner ones, with their anthers still closed, curve inwards over the carpels, the stigmas of which cannot be pollinated because they are not yet receptive. When later the inner stamens become dehiscent they bend outwards away from the carpels, and with these inner stamens now out of the way access to the stigmas is possible, but there is no doubt that self-pollination must also take place from laggard stamens. Protandry, however, is strongly developed, and is far more effective in the more advanced types of flowers such as occur in the family *Compositæ.* If the capitulum inflorescence of the Dandelion (*Taraxacum officinale*) (fig. 60) or the Daisy (*Bellis perennis*) (fig. 61) is examined, it is found that the younger florets at the centre of the inflorescence are actively discharging pollen whilst their stigmas are still protected, but in older florets, at the margin of the capitulum, the stigmatic lobes are elevated above the anthers but exposed for the reception of pollen brought to them from younger florets. Pollination may thus be effected when flies travel over the capitula, but should any florets be missed the stigmatic arms will curve round until they come into contact with pollen from the same floret. In the absence of insects or when insect visitation fails, self-pollination is often resorted to in many types of flowers which are structurally adapted to favour cross-pollination.

The condition of protogyny is not so common. Examples of it are the Figwort (*Scrophularia nodosa*) (fig. 59), the Sedges (*Cyperaceæ*) (fig. 62) and the Rushes (*Juncaceæ*) (fig. 64). In the Woodrush (*Luzula campestris*) of the latter family, for example, the brown, bract-like perianth opens just sufficiently to allow the feathery stigmas to protrude; the anthers at that time are closely imprisoned by the perianth segments. Later, when the perianth is expanded, the stigmas are withered and the large yellow anthers are fully exposed, thus enabling pollen to be conveyed from older flowers with exposed anthers to younger flowers with exposed stigmas. It is worthy of note that wind-pollinated flowers are usually not furnished with nectaries, nor are they attractively coloured. For the most part they are brownish like the Woodrush flower, or green as in the Grasses, all of which are wind-pollinated. Though cross-pollination is rendered possible in the Grasses owing to the anthers being carried on long and pendulous filaments which are often thrust far away from the stigmas, yet self-pollination must obviously take place in many types. Indeed, self-pollination appears to be the rule in some of the valuable cereal grasses, e.g. wheat. Wide experimentation in plant breeding has, however, established the fact that in the majority of the Grasses cross-pollination appears to be essential for fertilization.

Anemophily occurs in most of our commoner trees. In the wind-pollinated Poplars (fig. 36), the catkin inflorescences droop and are easily swayed about in the wind, whereas their near relatives the Willows have erect catkins furnished with nectaries and are visited by bees. The Poplar catkins are nectarless, as also are those of the Oak, Alder, Hazel, Hornbeam, Beech, Birch, &c. In these trees the loosely hanging catkins bear an abundance of pollen and are well exposed to catch the wind. There is, of course, great wastage of pollen by these plants, for wind-pollination is precarious and the chances for effective pollination are clearly not as favourable as in cases where pollen is conveyed directly from one flower to another by insect agency. Wind-borne pollen is dry and not sticky like that of flowers visited by insects, but once the dry pollen gets caught on the stigma which by its feathery nature offers such an expanse for its reception, germination of the pollen is immediate, for the feathery stigmas are really a system of richly branched glandular hairs affording safe anchorage and easy growth for the pollen tubes (figs. 62 to 64).

The flowers of some water plants, e.g. *Elodea*, the Canadian Waterweed, are diœcious and at pollination the staminate flowers break off as buds and appear at the water-surface to open and liberate their pollen; the stigmas of the carpellary flowers are brought to the surface by the elongation of the ovaries and may thus be cross-pollinated. Again, in the case of the Grass Wrack (*Zostera marina*), the pollen grains take the form of long threads which have the same specific gravity as the salt-water medium; the pollen may thus float freely at any depth and may become entangled in the diffuse submerged stigmas of the female flowers. Slugs and snails must obviously carry pollen on their viscid bodies when crawling over such dwarf-flowered plants as the Golden Saxifrage (*Chrysosplenium*).

Various types of specific adaptation, such as the " explosive " and " piston " mechanisms of certain flowers of the *Leguminosæ*, the " pollinia " of the *Orchidaceæ*, &c., demand examination of the complete flower, and their descriptions are best deferred until these flowers are studied practically (figs. 47 to 49, 70). Mention must, however, be made of certain types of flowers known as **cleistogamous**, which never open and which habitually resort to self-pollination. They are commonly found on certain plants, frequently in addition to the normal flowers, but they are greatly reduced in size and often concealed among the leaves. These tiny flowers are usually, but not always, destitute of petals; the walls of their anther lobes are very thin, and when the pollen grains germinate actually inside the anthers, the pollen-tubes pass through the anther wall directly into the stigma. Fertilization is accomplished in the usual way and viable seeds are formed. Cleistogamy occurs in many types, e.g. the Sweet Violet (*Viola odorata*) (fig. 42, H), the Wood Sorrel (*Oxalis Acetosella*), the Sundew (*Drosera*) and a few members of the *Leguminosæ*. In this family, the case of the Subterranean Clover (*Trifolium subterraneum*) is interesting; the small sealed flowers not only set seed in this way but the plant sows its own seeds; the stalk which carries the small pods becomes stiff and is stimulated to growth, as the result of which both pods and seeds are pushed into the ground.

CHAPTER VII

Fertilization

Pollination is a necessary preliminary to the more important act of the union of male and female nuclei in sexual fusion or **fertilization.** For the fertilization of all the ovules in an ovary there is usually a superabundance of pollen on the stigma; for every ovule there must be a pollen grain. The pollen grains are commonly in a binucleate condition before they leave the anther, for the single pollen nucleus soon divides to form a spherical, somewhat larger **tube** nucleus and a smaller curved **generative** or **antheridial** nucleus (fig. 28, C). The pollen grain is furnished with one or more thin areas or germ-pores in its thick outer wall to facilitate the growth of the thin, inner wall which emerges on the stigma to form a pollen tube. The stigmatic surface secretes a sugary fluid which helps in the early germination of the pollen grains. Pollen grains are easily germinated in a weak (five per cent) solution of cane sugar, and if they are suitably " fixed " and stained, the nuclei can be seen very clearly; the large tube nucleus is usually near the tip of the tube, with the elongated spindle-shaped generative nucleus close behind and surrounded by denser cytoplasm. The pollen tube in its extension through the style is assisted by the hollow or mucilaginous nature of the interior of this organ, but its path in the more solid type of style is by way of the intercellular spaces (fig. 31), and its extension is assisted by enzymic action. Nutriment for the growth of the pollen tube is supplied by the grain itself, which is rich in fats and proteins, and also by the stylar tissues in a manner somewhat similar to the exploitation of host tissue by parasitic fungal hyphæ.

After negotiating the tissues of the style, the delicate pollen tubes grow rapidly towards the micropyles of the ovules. This process often entails considerable elongation of the tubes, but during their extension through the long style a turgid condition is maintained in the tubes by the formation of cellulose plugs at intervals behind the nucleated contents. When the tubes leave the protection of the moist stylar tissues, they may continue their growth either within the wall of the carpel, or, if they enter the loculus of the ovary, may cling closely to the moist surface of the carpellary wall. In the flowers of the Shepherd's Purse (*Capsella Bursa-pastoris*), soon after pollination, the pollen tubes may be seen, after leaving the short style, to be closely associated with or even growing inside the funicles of the ovules, so that when they finally emerge into the loculus of the ovary their passage to the micropyles is very brief. In a few types, the pollen tubes may avoid the micropyle entirely, and reach the ovum by penetrating the ovule at its basal, chalazal end, this phenomenon being called **chalazogamy,** in distinction from **porogamy** when the tube enters normally at the micropyle.

When the pollen tube finally reaches its destination at the micropyle, its tip comes into contact with the tissue of the nucellus. By this time the depth of nucellar tissue over the micropylar end of the embryo-sac is very small, in many cases hardly more than the breadth of one cell-layer, so that the tube soon bores through this obstruction and finally penetrates the wall of the embryo-sac itself. What exactly guides the tip of the tube to the egg-apparatus is not known; it may be the function of the two synergidæ, appearing as they do one on each side of the ovum, to guide the tube towards the ovum. Meanwhile, the generative nucleus carried by the pollen tube has divided to form the two **male nuclei** or **gametes,** and the tube nucleus has disappeared (fig. 31, D). Penetration of the embryo-sac having been accomplished, the male gametes are discharged into the sac, one to fuse with the nucleus of the ovum, and the other with the "definitive" nucleus. *The first fusion constitutes true fertilization.* The union of the two haploid nuclei of **male gamete** and **female ovum,** each a product of the reduction phase, now *restores the diploid number of chromosomes* in the fertilized ovum or, as it must now be called, the **zygote.** The fusion of the definitive nucleus (the two polar nuclei united) with the other male gamete results in the so-called **triple fusion,** that is, the union of two female nuclei (the "polar") with one male gamete. Although this second union is subsidiary to the act of true fertilization with production of an **embryo** from the zygote, the triple fusion (a phenomenon which is peculiar to the Angiosperms) is nevertheless important, for it initiates the formation of the nutritive **endosperm** tissue.

The behaviour of the remaining contents of the embryo-sac, the three antipodals, varies considerably; in many types they disappear, whereas in others they form a quantity of nutritive tissue which probably assists in the nourishment of the embryo-sac until the endosperm is well established.

Fig. 32. Fertilization. Carpel of *Caltha palustris.*—Transverse section of mature carpel, showing an anatropous ovule ready for fertilization. Note embryo-sac and contents, the ovum with synergidæ on either side, directly below micropyle; the "definitive" (endosperm) nucleus in middle; the three antipodals facing chalazal region of ovule, all connected by cytoplasmic strands; surrounding the embryo-sac is the nucellar tissue. Integument on side of curved funiculus single, but on other side of micropyle double. Note narrow cells of vascular tissue passing through funiculus to chalaza. The carpellary tissue at ventral and dorsal sutures is supplied with stomata; vascular strand present in midrib or dorsal region. The two groups of epidermal hairs secrete nectar.

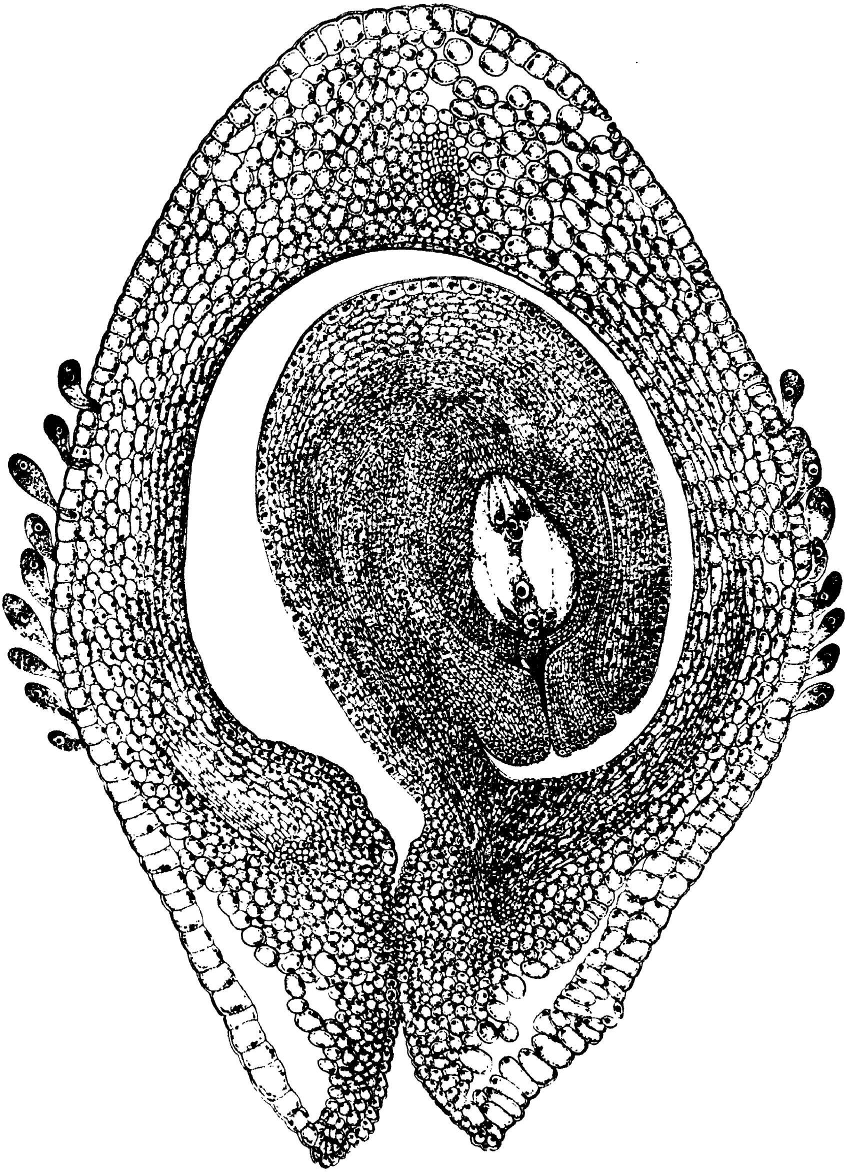

Fig. 32. (For description, see opposite)

CHAPTER VIII

Development of the Embryo and the Endosperm

As fertilization in the Angiosperm is a double process, it is necessary to follow the history of the triple or endosperm nucleus as well as that of the zygote. The development of the embryo from the zygote, however, is greatly retarded in comparison with that of the endosperm, and the formation of the latter will be taken first. In fig. 33, showing a section through the ovary of *Caltha*, the young embryo (in one of the two ovules figured) is in a one-celled condition but already surrounded by an appreciable quantity of endosperm. The " definitive " or endosperm nucleus divides so rapidly that the resulting nuclei lie freely in the cytoplasm, often accompanied by their nuclear spindles, and only after a large number of them have been formed do cell-walls arise between them. A large vacuole occupying the centre of the embryo-sac causes the first-formed nuclei to be pressed into position against the wall of the sac. and it is in this region that cell-walls first begin to appear to initiate the endosperm tissue. With continued division of the nuclei which are still free, the process of enclosing them with cell-walls progresses gradually towards the centre of the sac, where finally a small hollow indicates the end of the process. Some cells of the endosperm may enclose more than one nucleus, and such nuclei may fuse together, but what significance can be attached to these fusions is not known.

In the *Ranunculaceæ*, as in *Caltha*, and in many species belonging to diverse families, the endosperm forms a permanent tissue in the seed, so that the mature embryo embedded in it occupies but a small volume of the embryo-sac. Such seeds are called **endospermous** or albuminous. They are of frequent occurrence in monocotyledons (fig. 35) and in many families of dicotyledons which are somewhat primitive in their general evolutionary trend. In other dicotyledons (see below) the endosperm is, more or less, completely absorbed by the developing embryo which fills the whole seed. Such seeds are called **non-endospermous** or exalbuminous (fig. 34, G).

The development of the embryo from the zygote in the dicotyledon may best be illustrated by reference to the classical example of the Shepherd's Purse (*Capsella Bursa-pastoris*) (fig. 34). A longitudinal

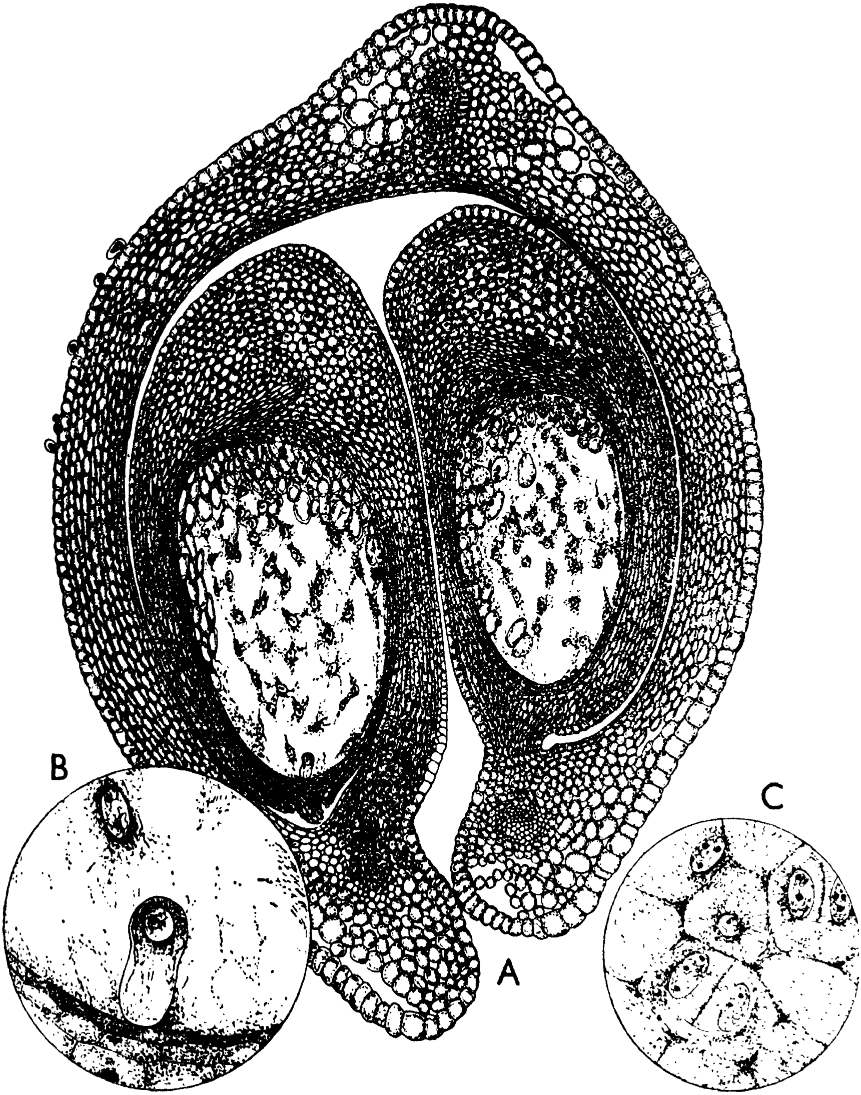

Fig. 33. Embryogeny.—A, young fruit (follicle) of *Caltha palustris*, showing early stages in seed formation (cf. fig. 32). In the two ovules there is active formation of endosperm by free-cell-formation; chalazal region of embryo-sac is partly obscured by disintegrating nucellar tissue; left-hand ovule shows fertilized ovum in position at micropylar end; note activity of the endosperm relative to that of the embryo which has not yet divided. B young embryo, slightly elongated, in position against wall of embryo-sac; an endosperm nucleus with two nucleoli is also shown. C divisions in endosperm and cleavage of cytoplasm at cell formation.

section of a very young fruit of this plant shows the fertilized ovules in possession of young embryos at practically the same stage of development; earlier and later stages, as depicted in the inset drawings in this figure, may be obtained from younger and older fruits respectively. The ovule in *Capsella* is of the folded, campylotropous kind in which the embryo-sac is curved like a horseshoe. The fertilized ovum, as usual, is situated facing the micropyle, and its first division takes place by a wall transverse to the long axis of the ovule. By further divisions parallel to this, a small filament of cells known as the **pro-embryo** is produced. Of these, the basal cell near the micropyle is oval in shape and much bigger than the others; its function appears to be that of fixing the pro-embryo in position at the micropyle. The cell at the other end of the filamentous pro-embryo, directed to the interior of the ovule, also grows in size but becomes spherical. This is the important **embryonic cell**; the rest of the pro-embryo (including the basal oval cell) is called the **suspensor.** It is from the embryonic cell that the whole of the **embryo**, with the exception of the root-tip, is developed (fig. 34, B, C). Though the system of suspensor cells remains in position at the micropylar end of the embryo-sac, it extends itself by further traverse divisions in order that the embryonic cell may become pushed more and more into the heart of the endosperm.

The initial divisions of the embryonic cell take place in orderly fashion. The first is median, in line with the filamentous pro-embryo; this is followed by a second vertical wall intersecting the first at right angles; a third wall which cuts both these vertical walls, transversely and equally, converts the spherical embryonic cell into eight equal-sized compartments or **octants.** Each octant divides by a wall parallel to the curved surface, so that there are now eight superficial and eight central cells within the embryonic cell (fig. 34, C, D). The superficial cells do not divide tangentially this way again, but do so actively by radial walls, i.e. at right angles to the curved surface. These surface cells remain throughout as a single layer and constitute the future epidermis of the plant. The rapid extension of the epidermis by repeated radial divisions proceeds in order to allow for cell division and general expansion of the central cells. Owing to the formation of another tangential wall in each of the latter cells there are now an outer and an inner series, so that the spherical em-

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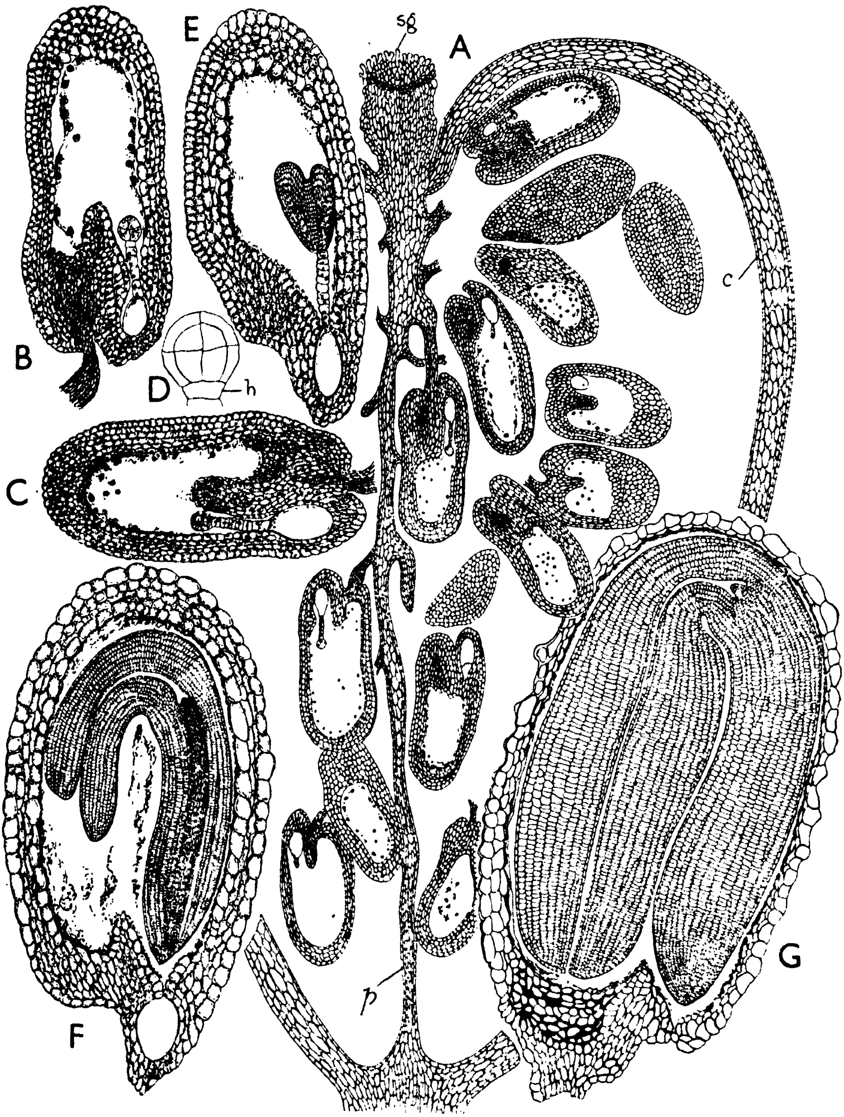
Fig. 34. Embryogeny (Dicotyledon).—A, longitudinal section of young fruit of Shepherd's Purse (*Capsella Bursa-pastoris*). Young embryos at stage shown in B; note young pro-embryos showing large end cell of suspensor fixed at micropyle; the filamentous suspensor carries terminal spherical embryonic cell into embryo-sac, which is lined with endosperm; embryonic cell in octant stage. Stages C to F from older fruits. C slightly older form of pro-embryo than B, showing more divisions in suspensor and also in octants (D). E two cotyledonary lobes derived from anterior octants; narrower posterior region includes last cell of suspensor ("hypophysis", *h* in D) to



form root-tip; note internal differentiation, indicating central plerome and periblem tissue external to it. F advanced stage, showing disappearance of suspensor; note marked development of radicle with root-cap and internal differentiation of vascular and cortical tissues; the two cotyledons are growing forward and curving at chalazal region; note growing point of plumule between cotyledons; endosperm almost completely absorbed. G almost ripe seed entirely filled by embryo (exalbuminous); left, the two cotyledons with plumule between; right, radicle with root-cap (vascular tissue omitted); note complete absence of endosperm. *c* pericarp; *sg* withered stigmas; *p* parietal placenta.

bryonic cell now consists of three layers of cells. The two layers of central cells, by repeated divisions in all planes, soon develop into a mass of small-celled tissue with the expansion of which the epidermis is constantly keeping pace. Even at these early stages of development, however, some differentiation can be made out within the young embryo, for the tissue derived from the inner central cells is seen to consist of elongated elements from which the future vascular system or stele is developed. Surrounding this region are the cells of the outer series, which are very uniform in appearance and become the cortical tissue of the adult plant.

Parallel with this development, the endosperm tissue (which, as in *Caltha*, grows in advance of the embryo) grows actively, and it is clear that the function of the suspensor is to push the embryo into closer and closer contact with this nourishing tissue. Unlike *Caltha*, however, the embryo of *Capsella* actively attacks the endosperm almost as soon as it is formed, and gradually assimilates its nutriment into its own system.

To return to embryonic development, the tissues within the four octants which are next to the suspensor grow quickly and the whole of this half-embryo soon becomes elongated to form both the root and the hypocotyl (the axis supporting the cotyledons). A small contribution to the root is made, however, from the last of the suspensor cells, called the **hypophysis** (fig. 34, D, *h*), which forms the root-tip. Except for this one small cell next to the embryo, the whole of the suspensor is a temporary structure; it may remain a while as a thin strand at the tip of the root, but it eventually disappears, its place being taken by the rapidly developing root. The position of the young root, therefore, is always at the micropylar end of the embryo-sac.

The tissues within the other four octants, which are directed towards the interior of the ovule, grow forward in a bilobed manner and the two lobes become the **two cotyledons** (" seed-leaves ") of the embryo (fig. 34, E). At the base of the groove between them, there arises a small protuberance of tissue which is to form the **plumule** or first bud of the plant (fig. 34, F). In the dicotyledonous embryo, therefore, the growing-point is *terminal*.

The progressive growth of the embryo within the embryo-sac is attended in *Capsella* by complete absorption of the nutritive endo-

Fig. 35. The Monocotyledon Embryo.—Longitudinal section of Grain of Maize (*Zea Mays*). Note single cotyledon, the scutellum *sc* in contact with endosperm *e* by means of epithelial layer *ep*. Growing point *gr* lateral to cotyledon. The plumule is protected by several leaves and finally by the coleoptile *cl*. The radicle *r* is also ensheathed within a root-sheath or coleorhiza *cr*. Stigma *sg*; pericarp *p*; testa *t*; aleurone layer *al*; stalk *st*. Insets: top, " horny " endosperm; cells with dense starch grains; below, " mealy " endosperm; cells with larger starch grains, which show gradual assimilation in vicinity of epithelial layer.

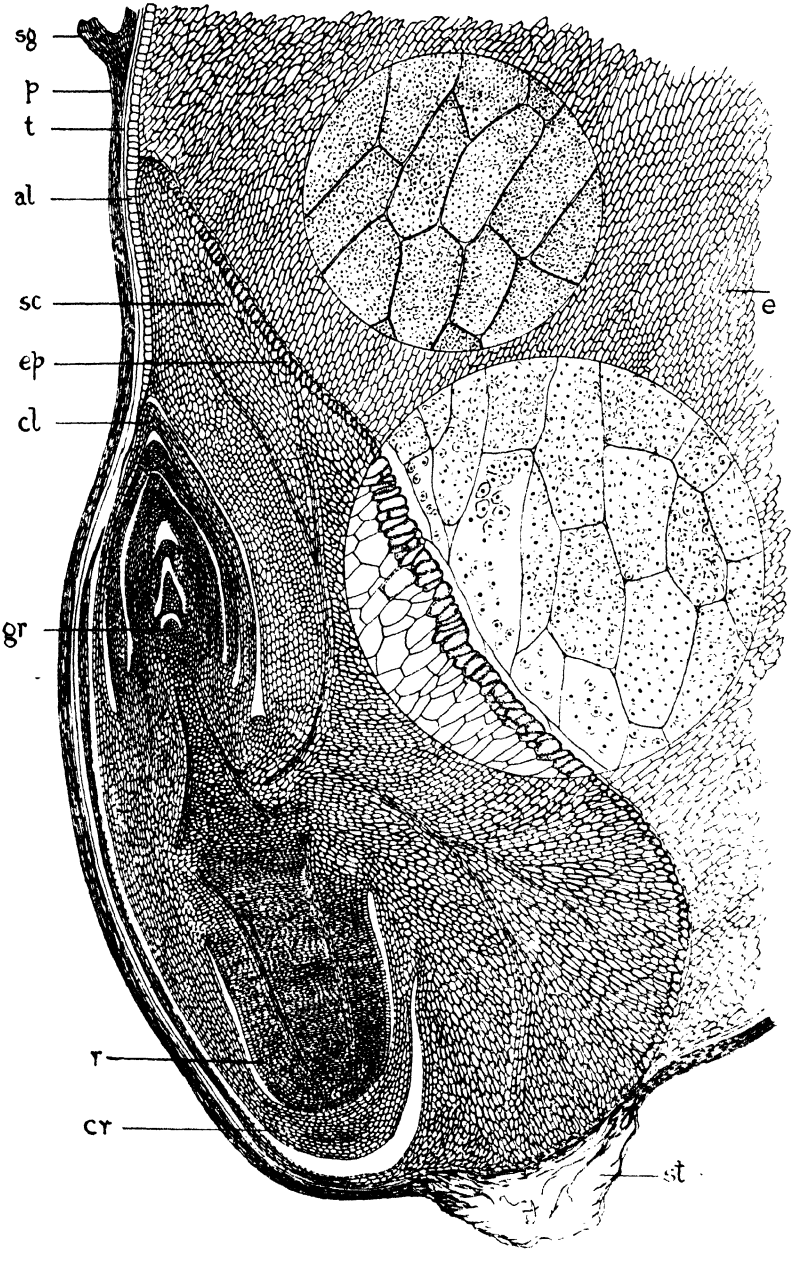


Fig. 35. (For description, see opposite)

sperm. The embryo thus comes to occupy the whole of the available space and becomes curved in conformity with the shape of the sac itself (see fig. 34, G). The root remains in position at the micropyle, and the hypocotyl becomes curved from more active growth on its outer than its inner side, so that the two cotyledons, closely apposed together, are pushed forward to accommodate themselves in the antipodal region of the embryo-sac. The seed is thus completely occupied by the embryo (**exalbuminous**).

The expansion of the embryo-sac in keeping with the growth of the embryo usually entails the complete disappearance of the surrounding nucellus, so that this tissue is gradually crushed out during the later phases of embryonic development. In some cases, however, e.g. the Stitchwort (*Stellaria Holostea*) (fig. 43, F) a variable amount of nucellus remains as a bulky tissue called the **perisperm,** whereas the endosperm has been absorbed during development.

During the maturation of the ovules into seeds, other significant changes are initiated in preparation for a period of rest. When the organization of the embryo is complete, the seed makes provision for hibernation, during which it may have to withstand adverse conditions and the rigours of winter. To this end, the seed gives up a great deal of its moisture, and the outer layers, namely those of the integuments, become tough, horny, or leathery. The hardened layers of the single or double integument, as the case may be, are then called the **testa** of the seed. Other minor changes that may occur result in the permanent swelling of a part of the testa near the micropyle to form a lump or **caruncle** (storing oil) as in the Violet (fig. 42, G); or some of the superficial cells of the testa may grow out into hairs, which later become air-filled owing to loss of water and then appear white, e.g. the cottony hairs growing on the seeds of the Poplar, Willow, and Cotton, whereby these seeds are dispersed through the agency of wind.

The problem of laying up a reserve of food in the resting seed is an important one. The storage consists mainly of insoluble materials in the form of minute starch grains, protein granules and fats. These materials are stored either in the endosperm or in the embryo itself.

The above description of embryonic development, as illustrated in *Caltha* and *Capsella*, is typical of dicotyledons. In the monocotyledons, however, there are fundamental differences, and within this group there are divergent lines of development. The embryo of the Maize (*Zea Mays*) (fig. 35) is fairly typical of monocotyledonous structure. The chief difference from the dicotyledon is, of course, the presence of only **one cotyledon.** In fig. 35, showing a section of the grain of Maize, the single cotyledon consists of that part of the embryo, known as the **scutellum,** which is in contact with the endosperm and from which it is separated by a glandular layer of cells, the **epithelium.** The plumule is *lateral* to the scutellum and is protected by a sheath called the **coleoptile;** the radicle is also enclosed in a sheath, the **coleorhiza.** In most monocotyledons the endosperm remains as a bulky tissue which, in the cereal grains of the Grasses, forms a valuable economic product.

Whilst fertilization of the ovule and its conversion into a seed is the normal procedure in the majority of flowering plants, there are instances where plants appear to form seed without utilizing the ovum and accordingly without the intervention of fertilization. This phenomenon, called **apomixis,** is reminiscent of apogamy in some of the Ferns, in which a young sporophyte plant may arise from the tissues of a prothallus formed from an abnormal spore which has not passed through the reduction phase. The young fern, therefore, arises from diploid prothallial tissue. A similar abnormality in the ovule is caused by some of the nucellar tissue budding inwards and penetrating the embryo-sac, within which it forms an embryo bearing some resemblance to that normally produced. It may be recalled that the nucellus is a diploid tissue, so that the abnormal embryo is likewise diploid. Instances of this peculiar method of seed formation are reported in certain species of Bramble (*Rubus*), Rose (*Rosa*), Hawkweed (*Hieracium*), and Lemon (*Citrus*). Another form of abnormality, again, with its parallel in the Ferns, is **parthenogenesis,** where an embryo may develop from an ovum which has not been fertilized, so that the seed remains haploid. Haploid seeds may germinate successfully, but the plants are small and sterile, and never attain the stature and vigour of normal plants; they are known to occur in a few members of the Potato family (*Solanaceæ*). Another feature, known as **diploid parthenogenesis,** may arise when an embryo-sac mother-cell omits meiosis in its tetrad division and forthwith becomes an embryo-sac with the usual contents. In this case, the ovum, being already diploid, develops into an embryo without the inclusion of a male gamete.

The more familiar cases of seedless fruits, as in the Banana and Orange, result from mere pollination of the stigma being apparently a sufficient stimulus to the formation of fruit without recourse to fertilization.

Sometimes seed and fruit may be dispensed with altogether. It occasionally happens, particularly in certain Grasses such as *Poa*, *Festuca*, &c., that under certain environmental conditions the inflorescence fails to develop normally, and in place of flowers in the spikelets small buds arise in a purely vegetative manner, become dislodged, and fall to the ground, to grow into plants of normal appearance. This phenomenon is known as **vivipary.**

CHAPTER IX

Fruits

Fertilization is not only instrumental in converting the ovules into seeds; its effects are also communicated to the carpels enclosing them, and not infrequently other parts of the flower may also be stimulated to growth. Petals and stamens, whose functions are obviously over, wither away, but the calyx often remains behind, with little increase in size, its presence no doubt affording some measure of protection to the ripening carpels. For the accommodation of the maturing seeds the ovary enlarges considerably, but the style and stigma gradually decay and disappear. When fully ripe the enlarged ovary, with its one or more seeds enclosed, is called a **fruit.** Whilst a fruit in the strictest sense is the product of a single ovary, in special cases where the floral receptacle has also been stimulated to growth it may include this part of the flower also. The floral types described in earlier pages reveal great diversity of structure, particularly in the character of the gynœcium—whether the carpels are free or joined; superior or inferior; bearing one or more ovules, &c. These structural differences are naturally reflected in a wide range of fruit construction.

The degree of protection afforded to the developing fruit depends largely upon the type of floral receptacle. In hypogynous forms like Buttercup and Wallflower the fruits are fully exposed when the outer protecting envelopes have withered away, but when the carpellary walls become dry and leathery ample protection is afforded to the fruits. Again, in the perigynous flower of the Rose, which possesses an urn-shaped receptacle, the small fruits within are well protected, for the receptacle becomes a permanent part of the fruit. It is, however, in the epigynous flower (inferior ovary) that the fruit receives its greatest protection. In this type the receptacular tube or cup becomes so intimately fused with the carpellary wall that the combined covering forms the wall of the fruit. The term **pericarp** is applied in general to the wall of the fruit, whether the covering is that of a superior ovary or an inferior ovary.

A fruit is said to be **simple** when it is the product of a single carpel or of a syncarpous gynœcium. In the family *Leguminosæ,* the fruit of a single carpel is called a **pod** or **legume;** it encloses a number of seeds along the ventral suture (fig. 47). It was pointed out (p. 33) that in the syncarpous gynœcium the various forms of ovary can be compared with two or more pod-like carpels which during development have fused together at their ventral sutures to form a single ovary and that this term can be applied to the gynœcium irrespective of the number of carpels composing it. From the point of view of the morphology of the fruit, the syncarpous ovary, like the single pod of the Pea, is also reckoned to be a simple fruit. A **simple** fruit may then be defined as the product of a monocarpellary or of a syncarpous gynœcium; this applies to the " superior " type of ovary, as in the Broom (fig. 47), Wallflower (fig. 41, F), &c., as well as to the "inferior" type, as in the Orchis (fig. 71), Iris (fig. 68), &c. On the other hand, the fruit of the Buttercup (fig. 1, J), or of the Bramble (fig. 50, I), is **compound,** because it is produced from an apocarpous gynœcium; that is, each of its several ovaries, remaining distinct from its fellows, forms a fruit by itself. Again, in the case of a fertilized capitulum of a member of the *Compositæ,* as in the Dandelion, each floret forms its own tiny fruit, which being the product of a bi-carpellary syncarpous gynœcium, is strictly simple. But a fruiting " head " (the " clock ") of the Dandelion is derived from a whole inflorescence and not a single flower, and must therefore be called an **aggregate** fruit.

The foregoing account describes the main classes of fruits as **simple, compound,** and **aggregate,** the differences being based on apocarpy and syncarpy. These classes may again be sub-divided according as the fruits open to set free their seeds or not. It is obviously unnecessary that single-seeded fruits should open, as the dispersal of the fruit entails that of its seed, for the germination of which the pericarp merely has to decay. To this class of fruits which remain permanently closed, as in Buttercup and Dandelion, &c., the term **indehiscent** is given. In the case of many-seeded fruits, whether derived from a single carpel, as in the Pea, or from a syncarpous ovary, as in the Violet (fig. 42, G), Foxglove (fig. 58, F), &c., the fruits must open for seed dispersal; they form another large class of **dehiscent** fruits. It is, however, necessary to distinguish an intermediate class, called " separating " or **schizocarpic** fruits; here the carpels of the syncarpous ovary *separate* from one another, but being individually one-seeded they remain closed or indehiscent (figs. 54, H, J; 57, G).

As the fruit approaches maturity, the pericarp undergoes profound changes. It may either become very dry, in the same way as the testa of the seed, or it may be stimulated to growth and enlarge into a bulky tissue which becomes progressively softer or fleshy as the fruit ripens, e.g. Cherry, Tomato. This difference in the texture of the pericarp again affords a useful means of classification of the great majority of fruits into **dry** or **succulent** kinds.

In the class of **dry-indehiscent** fruits, which, as was stated above are one-seeded, the commonest type is the **achene**, e.g. Buttercup (fig. 1, J), *Geum* (fig. 51, F), Clematis (fig. 38, I), Dandelion (fig. 60, E), in which the pericarp is tough and leathery but not hard. When the pericarp is very hard, as in the Hazel, the fruit is called a **nut.** A special kind of achene, known as a **grain** or **caryopsis**, occurs in the Grasses (*Gramineæ*), e.g. Maize (fig. 35), Wheat, Oat, in which the testa and pericarp are fused together, whereas in the true achene these layers are distinct.

The class of **dry-dehiscent** fruits is a large one. It includes those derived from single carpels, as in the *Leguminosæ* (e.g. Broom, Gorse, Lupin) where the fruit opens along *both* dorsal and ventral sutures, in which case it is called a **pod** or **legume.** If the fruit of a single carpel opens along *one* side only (the ventral suture) it is called a **follicle** (e.g. Larkspur, Marsh Marigold (fig. 39, E), Christmas Rose). The commonest type of dry-dehiscent fruit, however, is the **capsule**. It is the product of a syncarpous ovary, which may be " superior ", e.g. Violet (fig. 42, G), Red Campion (fig. 46, E), Foxglove (fig. 58, F), or " inferior ", e.g. Iris (fig. 68, I, J), Daffodil, Orchis (fig. 12, D). Somewhat specialized types of capsules consisting of two carpels occur in most members of the *Cruciferæ* family, e.g. Wallflower (fig. 41, F) and Shepherd's Purse (Frontispiece); in the former the capsule is long and narrow (a **siliqua**), in the latter flat and heart-shaped (a **silicula**).

In the class of **succulent** fruits, the fleshy pericarp grows to many times the size of the ovary. In some forms it becomes soft throughout, so that the seeds are embedded in a mass of soft pulp, e.g. Tomato (fig. 56, G), Gooseberry, Orange, Banana, Cucumber, all of which are **berries** of various types. The so-called " stone " fruits form another class of succulents; they are known as **drupes.** Unlike that of a berry, the pericarp of a drupe does not become softened throughout; it becomes differentiated into three layers, the thin skin or *epicarp*, the middle, soft portion or *mesocarp*, and the " stone " itself, or *endocarp* (fig. 52, D). The stone of a Cherry or Sloe, for instance, is therefore not the covering of the seed (which has its own thin testa) but the hardened inner layers of the pericarp. The examples named above are simple drupes produced from single carpels; compound drupes, like compound achenes, are the products of an apocarpous gynœcium, e.g. Bramble, Raspberry, Loganberry, in which each tiny fruit, called a **drupel**, is identical in structure with a drupe.

The fruit of the Apple (fig. 53, C, D) or Pear calls for separate consideration, as it shows features common to both berry and drupe. The gynœcium in these types is originally syncarpous (fig. 53, B), but during the ripening of the fruit the inner carpellary walls become tough like parchment (the " core "), somewhat like the stony endocarp of a drupe, and the remainder of the pericarp becomes the fleshy edible portion which during growth wedges the carpels apart. When the ripe apple is cut transversely the core appears as if formed from an apocarpous gynœcium, but the fruit is not a compound one. The special term **pome** is applied to these fruits.

There are, again, certain types of fruit which show characters intermediate between dry and fleshy. The Walnut, for instance, in its familiar form is only the stony endocarp containing the seed, but the whole fruit consists, in addition, of a soft pericarp which splits open at maturity (in the fleshy fruit the pericarp decays); " preserved " walnuts consist of the entire green fruit collected before the endocarp becomes hard. The prickly, capsular fruit of the Horse-Chestnut, again, is somewhat succulent, but opens into three parts or valves along the dorsal sutures; each of its three ovary-chambers contains two ovules, but generally only one in the whole ovary develops into the familiar brown smooth-skinned seed.

A fruit is said to be a " false " fruit or **pseudocarp** when, in addition to the ripened carpels, it includes the modified receptacle as well. In the " hip " of the Rose, the urn-shaped receptacle changes colour from green to red; it becomes enlarged and succulent and encloses the true fruits, which consist of a number of achenes (fig. 50, E). In the Strawberry, the true fruits are the tiny achenes depressed into the surface of the greatly swollen and succulent receptacle, the whole constituting the pseudocarp of the Strawberry.

A " separating " or **schizocarpic** fruit is the product of a syncarpous gynœcium, which may be inferior, as in the *Umbelliferæ* (fig. 54), or superior, as in the *Labiatæ* (fig. 57). It may split into as many parts as there are carpels, and each part, being one-seeded, remains closed like an indehiscent fruit. The bi-carpellary inferior ovary characteristic of the umbelliferous flower splits into two one-seeded parts, each called a **mericarp** (fig. 54, J). The superior schizocarp of the labiate flower consists originally of two carpels each containing two ovules, but eventually the fruit is divided by a second wall at right angles to the septum, the ovary thus becoming four-chambered, with one seed in each chamber. The pericarp becomes hard, and each fourth part, called a **nut** or **nutlet,** is therefore a one-seeded half-carpel derived by splitting. The whole fruit of four nutlets, characteristic of the *Labiatæ*, is retained within the calyx-tube and is called a **carcerulus** (fig. 57, G).

There are a few instances of the flowers of a whole inflorescence contributing to the formation of a common fruit or **infructescence.** A Pine-apple, for instance, is derived from an entire inflorescence together with the fleshy axis, which continues its growth into a leaf-bearing portion, the whole being called a **sorosis.** The Mulberry, derived from a spike of flowers, is somewhat similar; the perianth together with the ovary becomes fleshy, the whole fruit bearing a strong resemblance to the compound drupels of the Bramble, but differing from that type in that it is the product not of a single flower but of a whole inflorescence. The **syconus** of the Fig consists of a hollow fleshy infructescence enclosing numerous drupels each produced from a tiny carpellate flower. Closely akin to the Fig is *Artocarpus*, whose huge inflorescence fructifies to form the edible " bread fruit " of the tropics.

These structural differences in fruits are naturally related to the mechanisms which play a part in the dispersal of their seeds, and the numerous devices whereby this is effected must now be considered.

CHAPTER X

Dispersal of Fruits and Seeds

It is a matter of common observation that far more seeds are produced than can ever find room to grow. A Hawthorn bush or a Rowan tree laden with its reddish fruit, an Elm or a Sycamore bearing a host of winged fruits, a Foxglove or an Orchis furnished with numerous capsules each containing hundreds of seeds, are striking evidence of the enormous productivity of flowering plants. To ensure any measure of success in germination, fruits and seeds must be transported from the vicinity of the parent plants, and there are many devices by which their dispersal may be effected. Their ultimate success in germination depends upon various factors, amongst which the more essential are access to open space and light and an environment suitable to the needs of the plants. Overcrowding—the great majority of seeds under natural conditions fall around the parent plants—no doubt results in great destruction of young seedlings. Under conditions of cultivation, the common practice of transplanting and thinning out young plants ensures reasonable spacing-out, which assists root extension and better feeding, free circulation of air and better exposure to light for photosynthesis. All are necessary if the plants are to be healthy.

Wind is the principal agency for effecting the dispersal of fruits and seeds. Some seeds, like those of the Foxglove and common Orchis, are so numerous, small and light that they may be carried in air currents, just like pollen. A very common adaptation for dispersal by wind is the development of fine silky hairs which act like a parachute and bear the tiny fruits aloft. The achenes of the Dandelion and of many other members of the *Compositæ* are furnished with a " pappus " of hairs; the achenes of *Clematis* have hairy styles. Sometimes it is the seed and not the fruit which is furnished with long hairs, e.g. the Willow and Cotton; these hairs grow from the wall of the testa, and in the Cotton-plant the hairs form the raw cotton of commerce. Heavier wind-borne fruits need a more elaborate mechanism. They are provided with one or more wings, which are usually post-fertilization growths of the pericarp, e.g. Ash, Elm, Sycamore. These are known as **samara** fruits. Many of the schizocarpic fruits of the *Umbelliferæ* have their margins expanded into thin membranous wings which keep them aloft and delay their fall.

In the opening of dry fruits of the capsular variety, various interesting mechanisms are found. Their seeds escape by the opening of the pericarp along the ventral or dorsal suture or both. When dehiscence is effected, the separating parts of the capsular wall are called **valves,** and their number usually corresponds with the number of constituent carpels. Thus, in the tri-carpellary fruits of Iris (fig. 68, J), Hyacinth (fig. 66, C), and Violet (fig. 42, G) the lines of dehiscence lie along the dorsal sutures and thus open directly into the loculus; each of the three valves thus comes to consist of two neighbouring half-carpels, with one or more rows of seeds, which in the Iris and Hyacinth occur on each side of the disrupted partitions, but in the Violet on each side of the placental ridges. The bi-carpellary fruit of Foxglove (fig. 58, F) opens along the ventral grooves, and the two boat-shaped valves break away from the partition between them, leaving the very numerous small seeds exposed on the large cone-shaped axile placenta; when the Foxglove plants are agitated by wind the seeds are jerked out of their capsules and they are light and small enough to be carried away by the wind. Mention has already been made of the two-valved siliqua and silicula fruits of the *Cruciferæ.* These open along the two ventral grooves from below upwards, exposing the seeds on a wiry frame (the *replum*, fig. 41, G) across which is stretched a thin, papery partition; their seeds are somewhat flattened and may be conveyed by wind. The behaviour of the siliqua fruit of the Hairy Bitter-cress (*Cardamine hirsuta*) is of interest; just before dehiscence, the dried valves are in a state of tension, and when they begin to open from the base the valves coil up suddenly like a watch-spring, a process which results in the seeds being flung several feet away. Other quick-acting or explosive mechanisms due to differential tensions within the tissues of the drying pericarp occur in leguminous fruits, e.g. Broom, Gorse, in which the double splitting at the two sutures is followed by a rapid twisting of each valve, the sudden operation bringing about effective dispersal of the seeds which are attached to the margins of the valves. Again, in the capsule of the Violet, the three boat-shaped valves curl their margins inwards, and as the seeds are exceptionally smooth the pressure of the incurling margins causes the seeds to be forcibly ejected.

The dehiscence of other capsular fruits may not extend the whole length of the sutures, but often only half-way down or even less, so that the partial valves appear like a number of apical teeth. The tri-carpellary fruit of the Stitchwort (*Stellaria Holostea*) splits from the top into six teeth which extend half-way down along both sutures (fig. 43, E). In the Primrose (*Primula vulgaris*) the five-carpellary capsule (accompanied by its enlarged calyx) opens first by five recurved teeth which divide again to form a double series. In the Red Campion

(*Lychnis dioica*) the ripe capsule has twenty teeth derived from the division of five, which is the number of carpels in the pistil of this flower (fig. 46, E). These toothed capsules are frequently hygroscopic, widely open in dry weather and partially closed in wet weather. Their stalks become stiff and wiry, and when the plant is shaken by wind, the seeds are dislodged and ejected from the capsule. In the capsular fruits of the Poppy (*Papaver* sp.) and the Snapdragon (*Antirrhinum*) there are a number of pores near the top through which the dry seeds are jerked out. A few instances occur where capsular dehiscence is transverse or equatorial, as in the Scarlet Pimpernel (*Anagallis arvensis*), the fruit of which opens by a lid, leaving the seeds exposed on a central placenta in the lower half.

Animals may also assist in the dispersal of certain fruits by carrying them on their coats. These fruits are provided with various contrivances, such as barbs, hooks, or stiff bristles, which cling to the coats of the animals. These barbs, &c., almost invariably develop on the pericarp of the fruit and rarely on the seed-wall. In the Water Avens (*Geum rivale*) (fig. 51, E) the long style after fertilization bends back about a third of its length from the top, and when this terminal part breaks off, the remainder of the style ends in a small hard hook. The familiar Cleavers (*Galium Aparine*) has its fruits covered with small hooked hairs, and again, in the big-leaved Burdock (*Arctium Lappa*), a member of the *Compositæ*, the tips of the involucral bracts are strongly recurved to form very efficient clinging organs.

Succulent fruits are attractive and palatable to many kinds of birds. The ripening processes which go on during the softening of the pericarp make the tissues sweet to the taste and there is also a change in colour from green to the more attractive red, as in the Cherry, Plum, Tomato, &c.; similar processes also take place in the "receptacular" fruits of the Rose, Strawberry, &c., but here it is the receptacle, and not the actual fruits, that changes colour. When the birds feed on the juicy pericarp or receptacle, as the case may be, the seeds may be retained on the beak and conveyed some distance away before being rubbed off, or they may be swallowed and carried internally. Seeds such as those from the various types of berries are furnished with hardened testas; small fruits, like the tiny achenes on the red receptacle of the Strawberry, or inside that of the Rose, are swallowed entire; they are similarly possessed of a toughened outer coat, here the pericarp, and pass through the alimentary canal without injury.

Birds are also responsible for transporting seeds in soil adhering to their feet. Squirrels, ants and mice, when making up their winter store, are instrumental in the dispersal of certain fruits of the nut variety.

The seeds of some plants, e.g. Violet, Spurge, are furnished with spongy outgrowths on the testa, called *caruncles*. These bodies are rich in oil and are much sought after by ants, which discard the seeds without injuring the embryo.

Dispersal of fruits and seeds through the agency of water is not very common. Such types are usually provided with abundant air spaces either within the tissues of the pericarp or those of the testa. The fruit of the Coconut (*Cocos nucifera*), for instance, is furnished with a fibrous and woody pericarp, the inner layers of which are very hard (the " shell " of the shop coconut); the thin testa covering the white and edible endosperm encloses a large cavity containing milky fluid; the fruit is buoyant and capable of floating long distances, and this may account for the prevalence of the Coconut Palm in the vegetation of marine islands. The large berry of the Yellow Water-Lily (*Nuphar luteum*), when ripe, breaks off from its stalk and splits into separate carpels; air bubbles imprisoned in the slimy wall of the carpels keep the seeds afloat, and when the carpels decay the seeds sink. The seeds of the White Water-Lily (*Nymphœa alba*) are furnished with a spongy aril and air spaces are present in the testa; the fruit ripens under water and when it dehisces the seeds reach the surface and drift about until the spaces become waterlogged and they sink. The fruits of the Pondweed (*Potamogeton*) are also supplied with an aerated pericarp and may thus be carried on the surface of the water before they sink. The seeds of *Crinum* (*Amaryllidaceœ*) have a thin corky covering which renders them buoyant and waterproof during dispersal by water.

CHAPTER XI

Heredity and Evolution

From time to time, many theories of heredity have been advanced which seek to explain how *like* begets *like,* and sometimes also *unlike.* Darwin (1859) based his great theory of evolution on three outstanding principles, namely, variation, heredity, and the struggle for existence. He had observed how man is able to modify the characters of domestic animals by constantly selecting and breeding from those showing certain desirable qualities, and to a similar process going on in nature he gave the name of natural selection. He saw that however close the relationship and resemblances between one organism and another are, there are also differences between them. Such differences he called variations. Moreover, he observed that under natural conditions competition is keen and mortality very high among young plants of similar kind and similar wants. Nature is constantly " selecting " those plants or organisms which are better adapted for existence, and in course of time those which fail to adapt themselves tend to disappear. Natural selection appears to favour those plants which respond in the right way in a given environment. Evolution, accordingly, finds expression through selection acting on variations. Some forms of variation are better endowed to meet the conditions of the environment and are selected; others which are incapable of adjusting themselves to these conditions are rejected.

We cannot, in this brief review, enter further into Darwin's great contributions to evolution, but must now consider a hypothesis which is acclaimed as the foundation on which our extended knowledge of heredity and the modern science of genetics are established. This theory is known as Mendelism. It is based on the work of Mendel, an Austrian abbot, which, though dating back as far as 1866, was practically unknown to the scientific world until 1900, when by a remarkable coincidence it was rediscovered by other famous biologists independently.

To introduce the Mendelian theory we must refer again to the methods of pollination. In the plant we have seen that the gametes are present in pollen and ovule, and that fertilization of the ovules is dependent on pollination. Under natural conditions when both self- and cross-pollination are operative, we cannot with any degree of accuracy study the heritable properties and the distribution of heritable factors in the plant. With the plant breeder's control of pollination, however, together with the exact knowledge gained by the cytologist in his study of gametic cells and their intimate structure, it is now possible to get a very clear insight into hereditary properties and the mechanism of inheritance in plants.

The plant breeder, employing exact methods (p. 134), will self-pollinate a plant by transferring pollen from anther to stigma in the same flower, or from one flower to another on the same plant. He sees that the stigma is ripe for the pollen, and if a flower is so strongly protandrous as to be devoid of pollen at the right time, then pollen must be conveyed from another flower (at pollen-shedding stage) on the same plant. There are, however, many plants (e.g. Sweet Pea, Bean) whose flowers are able to pollinate themselves, because the anthers and stigma are so situated that self-pollination is spontaneous. Even with this type of flower it is well to guard against the risk of cross-pollination, by protecting the plants against insect visitation.

If a plant self-pollinated from generation to generation gives rise to offspring which are all alike, then that plant is said to *breed true* and its progeny is known as a *pure line.* While the ideal in the mind of the breeder is to produce a race of plants true to all desirable properties, experience shows that this can hardly, if ever, be achieved in practice. We speak, then, of a pure race in reference to one or more *characters*, as, for instance, constancy of flower-colour, height of plant, shape of leaf, resistance to disease, and so on.

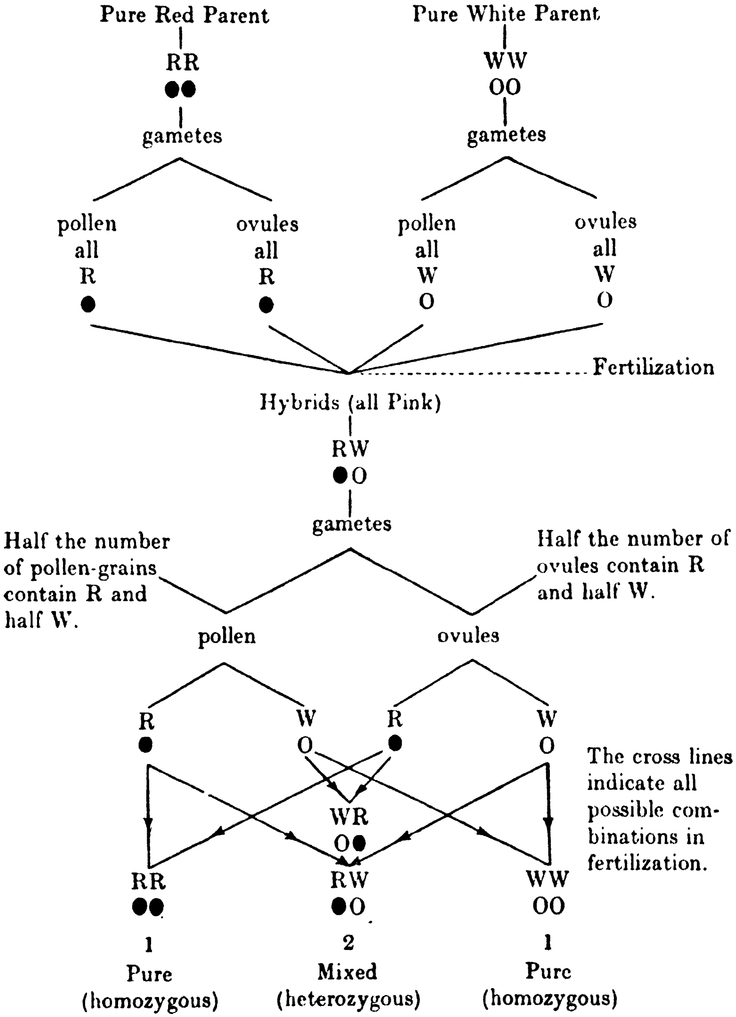
The fact that the individuals of a pure race are all alike in one or more characters is due to the complete identity in the germ cells (gametes) of certain factors which govern these characters. If a plant breeds true to flowers coloured red, then the factors for colour are " red " in all pollen grains and ovules. The factor must be the same in the male gamete and in the female gamete. If the colour-factor is denoted by the letter R, a pollen grain bearing R will fertilize an ovule bearing R, and the constitution of the zygote, as RR, indicates the purity of the race, as far as colour of the flowers is concerned. An individual which breeds true to one or more characters is called a **homozygote,** or is said to be **homozygous** for that character.

In reference to the progeny of a pure race, it is inferred that cross-pollination between homozygous individuals results in the same type of offspring as if the individuals were self-pollinated. This aspect of " crossing " is known as inter-pollination, or to use a genetical term, *in-breeding.* (For the maintenance of a pure race of plants grown on a large scale, the method of inter-pollination is frequently adopted (p. 137); as long as the pure strain is well isolated from other compatible strains, the risk of pollen contamination is very slight.)

If the seeds collected from a self-pollinated plant give rise to individuals which are not alike, then the plants are said to *segregate.* This may be illustrated by considering the progeny obtained by cross-pollinating two pure races. Suppose a pure race of red-flowered plants is crossed with a pure race of white-flowered plants. It is immaterial whether pollen is conveyed from a red flower to the stigma of a white flower or from a white flower to the stigma of a red flower; that is, it makes no difference which plant acts as the male parent and which the female parent, the results are the same (this does not hold in all cases of colour inheritance). The pure parental races may now be called *RR* and *WW*, for " red " and " white ", respectively. Under certain conditions of inheritance (discussed below) the descendant hybrid plants will *all bear pink flowers.* If the hybrid pink plants are now self-pollinated, their seeds will give rise, not to plants all with pink flowers, but to three kinds of plants, some bearing red, some pink, and others white flowers. Moreover, there will be approximately *twice* as many " pinks " as " reds " or " whites ", i.e. the plants will occur nearly in the proportion of 1 Red : 2 Pink : 1 White, and the larger the number of seeds sown the closer will be the approximation to this ratio. These three races having been segregated from the common " pink " ancestor, it now remains to self-pollinate all three races and collect their seeds. The progeny of the selfed " red " and also of the selfed " white " race are found to breed true, and will continue to do so repeatedly as long as they are submitted to self-pollination. The race of pink-flowered plants, however, does not breed true, but separates again in the same way and in the same proportion to give the red, pink, and white forms.

In view of the fact that the " pink " generation does not produce a pure race of pink but constantly segregates into the three distinctive types, two of which are pure, the conclusion is that there are only *two* factors governing the colour of all the flowers in this particular example, namely, *R* for " red " and *W* for " white ". For the pure race of red (*RR*) a pollen grain carrying *R* will fertilize an ovule carrying *R*, and for the white race (*WW*) a pollen-grain carrying *W* will fertilize an ovule carrying *W*, and we conclude that the pink types occur when *R* and *W* in pollen grain and ovule meet in fertilization to give the zygote *RW*. This type of zygote, which constantly segregates as above, is called a **heterozygote,** or is said to be **heterozygous** for a specified character (here colour). These conclusions may be symbolized as follows:

TABLE I



Half the number of pollen-grains contain R and half W.

Half the number of ovules contain R and half W.

The cross lines indicate all possible combinations in fertilization.

From the above diagram, which, it must be emphasized, is in respect of *one specified hereditary character* (and reserving consideration of other types of inheritance for the moment), the following important deductions are made:—

(*a*) A character (e.g. colour, height, &c.) is controlled by a **pair** of factors.

(*b*) A gamete can carry only **one** factor, here *R* or *W*.

(*c*) The two factors of a character remain **independent** in the zygote.

(*d*) The pollen grains of a **homozygote** are of **one kind** in any anther, and the ovules similarly of **one kind** in any ovary of a flower. Here they all carry *R*, or all carry *W*.

(*e*) The pollen grains of a **heterozygote** are of **two kinds** in any anther, and the ovules similarly of **two kinds** in any ovary of a flower. In any anther and in any ovary the two kinds occur in **equal numbers.** Here half the pollen grains carry *R* and half carry *W*; and likewise half the number of ovules carry *R* and half carry *W*.

In explanation of the ratio of 1 pure-red : 2 mixed (pink) : 1 pure-white, the pure races are obtained because there is only one kind of gamete in pollen and ovule, and therefore only one possible combination of these when they meet in a zygote, red or white, as the case may be, but in the mixed (pink) race, both of these gametes are present, in *equal* numbers, and the chances are equal that a " red " pollen grain may fertilize a "white" ovule, or a "white" pollen grain may fertilize a "red" ovule, so that there is double the number of *RW* heterozygotes.

In the above example of the hybridization of two pure races, it was stated that the colour produced in the hybrid was more or less intermediate between that of the parental types, pink being produced from red and white. While it is important to remember that the factors of a pair remain independent in the zygote, it is not the factors that change when as the result of hybridization a change is produced, but the *effect* produced by them when they meet in fertilization. Since the effect is a pink colour we conclude that the effect contributed by the factors is more or less intermediate between red and white. There are numerous cases of inheritance, however, where the effects of the two factors of a character are not equal, and there appear to be all grades of dominance. Dominance of one factor over the other may be so complete as to mask the effect of the other entirely, in which case we speak of that factor as **dominant** and its hidden partner as **recessive.** In the case of the production of pink flowers from the crossing of red and white, the factors exercising an intermediate effect are said to be incompletely dominant. As is explained below, the ratio of 1 : 2 : 1 just obtained no longer holds in cases where complete dominance is exercised.

Mendel looked upon a plant as an assemblage of *unit* factors, and the remarkable success of his experiments in the hybridization of plants was due to his working with one factor at a time. Previous investigators had failed to interpret their results because they were concerned with the plant as a whole, on the assumption that the attributes of both parents were combined in the hybrid generation to some degree intermediate to them both.

For experimentation Mendel chose the Garden Pea (*Pisum sativum*), for the reasons that he saw in this plant certain characters whose extremes were sharply differentiated and clearly established from one generation to the next. Among the various races of peas which he selected were tall plants which always bred tall; short plants which always produced short; the seeds which he sowed were either round or wrinkled; the cotyledons in some of the races were either yellow or green, and so on. These sharply distinctive features in these different races were repeated from one generation to another without change, that is, all the races *bred true.* His selection of the edible pea was a fortunate one, for it possesses a type of flower which under natural conditions habitually resorts to self-pollination. Thus he was able to maintain the purity of the various races for as many generations as he wished as long as the plants were self-pollinated.

One series of Mendel's experiments was concerned with the inheritance of height. He selected for parent plants individuals from races which were consistently tall or short, the former in the region of six feet and the latter never exceeding two feet in height. He was satisfied that these races in the normal manner of self-pollinated pure races bred true from generation to generation. For the crossing of individuals of these two races, one tall, one short, he removed the immature stamens from the flowers of a dwarf plant and conveyed pollen from the ripe stamens of a tall plant to the stigma of the dwarf plant, that is, the tall plant acted as the male parent and the dwarf plant as the female. He found, however, that it made no difference to his results if he used a tall plant as the female parent and fertilized it with pollen from a short plant (reciprocal crossing), taking, of course, the same precaution against self-pollination by cutting away the stamens of the flower pollinated. After cross-pollinating or hybridizing a very large number of flowers in this way, in due course he collected all the available seeds and found that they *all produced tall plants.* Furthermore, these hybrids were even taller than their tall parents. This phenomenon, which is known as *heterosis* or hybrid vigour, is difficult to explain, but it is a feature which is constantly experienced in genetical work; it is discussed again (see p. 136) in connexion with the merits of cross-fertilization.

It is remarkable that all the plants of the first hybrid generation (styled the *first filial generation*, or briefly, F_1) were tall; there were none of intermediate size to indicate that one of the parents was a short plant.

When these hybrids reached the flowering stage they were allowed to self-pollinate in their habitual way. Collecting and sowing the seeds of this hybrid F_1 generation, Mendel saw, however, that in the second generation (F_2) some of the plants were tall like the tall parents and others short like the short parents, but again, there were *none of intermediate size.*

From these experiments Mendel concluded that the factors for tallness and shortness were *alternative factors*, and since one of them (tallness) showed itself in the first generation to the complete exclusion of the other (shortness), Mendel called the factor for tallness **dominant** and that for shortness **recessive.** To such a pair of alternative factors Bateson gave the term **allelomorphs** (or **allels**).

When the proportion of tall plants to short was examined in the F_2 generation Mendel found almost an exact ratio of 3 talls to 1 short; and whatever the nature of the plant-character with which he worked, his figures for the F_2 generation were always in close approximation to this ratio for the dominant and recessive factors respectively.

To return to the F_2 generation of tall and short plants, Mendel saw that if the factor for tallness was completely dominant, its absence from the short plants could be proved in two ways: (1) by allowing the short plants to self-pollinate, and (2) by crossing them with the pure recessive parent strain, a procedure which is known as *Back-crossing.* Whichever method was adopted, the resulting plants all turned out to be short like the parents. If precautions were taken that they were always self-pollinated, generation after generation of the short plants yielded short plants. Clearly, then, although the short plants were descended on one side from a tall ancestor, the factor for tallness had been completely eliminated and the plants bred true to the original short stature.

Mendel next proceeded to analyse the tall plants of the F_2 generation, which as stated turned out to be three times as numerous as the short. When their seeds were sown, one in every three of the resulting plants of this, the third or F_3 generation, as long as they were left to self-pollinate, bred true to tallness, just as the short ones bred true to shortness. The remaining plants (i.e. the "two-in-every-three"), however, turned out to be a mixture of tall and short. When the experiment was continued with these mixed plants, always allowing them to self-pollinate, the recessive-short always produced short, but the tall plants again separated out in the ratio of one pure-tall: two hybrid-tall.

Hitherto we have called the two factors of a character by distinctive letters, such as *R* for *Red* and *W* for *White*; it is, however, the custom to employ the same symbol, for example, a capital *T* for *Tall* and a small *t* for *Short*, to express the factors for *Height.* In the case referred to above, of red and white factors for *Colour*, *Red* would be represented by *R*, and *White* by *r*.

To symbolize Mendel's results, let the dominant factor for tallness be represented by *T* and the recessive factor by *t*. The tall parents are denoted by *TT* and the short parents by *tt*, the doubling of the letters indicating the constitution of the zygotes.

The gametes of the tall plants will carry the factor *T* for tallness, and similarly the short plants will form gametes bearing *t* for shortness. When these gametes, carried as they are in both pollen and ovules, come together at fertilization, they form zygotes with the allelomorphic pair *Tt*, but since one factor *T* for tallness has been proved to be dominant over *t* for shortness, *all the first generation* of plants in the F_1 hybrid are tall. When, however, the hybrids form their gametes, they will produce in equal numbers some carrying the factor for tall and some the factor for short, but *no gamete can carry both factors of an allelomorphic pair*. The exact mechanism and significance of this process is discussed later, but here we repeat that it formulates the most important law of inheritance, namely, that the factors of an allelomorphic pair separate or segregate at the formation of gametes.

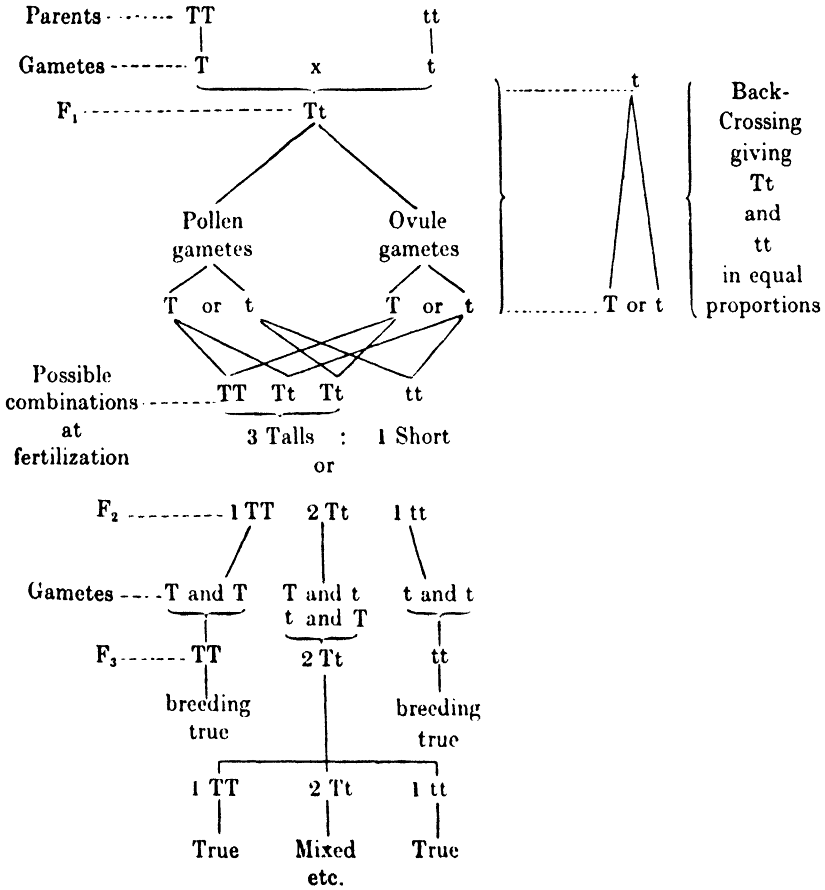
To return to the hybrid generation *Tt*, the gametes are either *T* or *t*, and they are formed in equal numbers in both pollen grains and ovules. Thus, some pollen grains will contain *T*, others *t*, and some ovules will contain *T*, others *t*. When the flowers are allowed to self-pollinate, the chances are equal that a pollen grain with a *T* will fertilize an ovum with a *T*; or that a pollen grain with a *T* will fertilize an ovum with a *t*; or that a pollen grain with a *t* will fertilize an ovum with a *T*; or that a pollen grain with a *t* will fertilize an ovum with a *t*. That is, the combinations possible are *TT*, *Tt*, *tT*, *tt*, or 1*TT*, 2*Tt*, 1*tt*. This may be symbolized as in Table II (p. 113).

The validity of the above deductions can be proved by the procedure already alluded to, of back-crossing (shown to the right of the above table), which consists in pollinating the F_1 hybrid plants with the original recessive parent stock. The F_1 generation, denoted by *Tt*, produces an equal number of gametes *T* and *t*, and if pollen from the pure-short parent, that is, the parent bearing *t*, is employed, the progeny are *Tt* and *tt*, so that an equal proportion of pure-short (*tt*) and mixed-talls (*Tt*) is obtained. In actual plant-breeding practice the procedure of " back-crossing " is a valuable one and is frequently resorted to in testing the purity of races.

Individuals which breed true (here *TT* and *tt*) are homozygotes, and they are homozygous for the factors of a specified character, namely, tallness or shortness; individuals which carry the pair of allelomorphic factors (*Tt*) are heterozygotes, and they are heterozygous for either of these factors. Heterozygotes, as previously stated, do not breed true but constantly segregate from one generation to another, according to Mendel's Law of 1 pure dominant, 2 mixed, 1 pure recessive.

Hitherto we have discussed the inheritance of only one pair of allelomorphic factors such as tall and short, and what has been

TABLE II



said could also have been illustrated by reference to any other character with which Mendel experimented. It is, of course, possible for an individual to be homozygous for one pair and heterozygous for another, and when we come to consider the working at one time of more than one pair of factors the case is more complicated, but the laws of inheritance are the same.

Combining two characters, say, *height of plant* and *shape of seed*, Mendel sowed round peas which gave tall plants, and wrinkled seeds which gave short plants. When he crossed the flowers of these plants, a round-tall with a wrinkled-short (again it was immaterial which was the male and which the female parent), all the seeds from the pods were round, the factor for round seed being dominant to that for wrinkled. Again, all the plants were tall, since tallness is dominant to shortness. The subsequent results which he obtained may be explained as follows. When the plants of this F_1 generation form their gametes they will have *four* different kinds in both pollen grains and ovules in which they exist in equal numbers. If, again, *T* and *t* represent tall and short and *R* and *r* round and wrinkled respectively, some gametes will carry the factors *TR*, others *Tr*, others *tR*, others *tr*, the capitals, as before, indicating dominant and the small letters recessive factors.

In fertilization, therefore, the gametes will meet at random in all combinations which can best be set out in the form of a divided square. By writing them at the top and side and multiplying the top set by each of the vertical set in turn, we get the composition of the zygotes shown in the small squares:

TABLE III

		POLLEN			
		TR	*Tr*	*tR*	*tr*
OVULES	*TR*	*TTRR* Tall-round	*TTRr* Tall-round	*TtRR* Tall-round	*TtRr* Tall-round
	Tr	*TTRr* Tall-round	*TTrr* * Tall-wrinkled	*TtRr* Tall-round	*Ttrr* Tall-wrinkled
	tR	*TtRR* Tall-round	*TtRr* Tall-round	*ttRR* * Short-round	*ttRr* Short-round
	tr	*TtRr* Tall-round	*Ttrr* Tall-wrinkled	*ttRr* Short-round	*ttrr* Short-wrinkled

Collecting the above results, and bearing in mind that the capitals *T* and *R* are dominant in any combination, we see that there are of tall-round, 9; tall-wrinkled, 3; short-round, 3; short-wrinkled, 1. Of the 9 tall-round only one is homozygous for both allelomorphs, namely, *TTRR*, like one of the tall parents; four are homozygous in one pair and heterozygous in the other pair, namely, two of *TtRR* and two of *TTRr*; there are four heterozygous in both pairs of allelomorphs, namely, four of *TtRr*. Each of the other groups has one homozygous in both characters, namely, one *TTrr*, one *ttRR*, and one *ttrr*, this last being homozygous for both the recessive factors and the same as the other parent, namely, short-wrinkled. The remaining squares are homozygous or heterozygous in one character, namely, two of *ttRr*, and two of *Ttrr*. In the whole system, the completely homozygous types are *TTRR* (like the tall parent), *ttRR** (short-round), *TTrr** (tall-wrinkled), and *ttrr* (like the short parent). Those marked with an asterisk have not only *the combined characters of the parents, but they will breed true, because they are homozygous.*

Homozygous individuals always breed true ; not so the heterozygous, which, as stated, split up into homozygous and heterozygous forms.

It is a property of the Mendelian Theory that by recombinations of the gametes new combinations in the zygotes are obtained. The new types, " tall-wrinkled " and " short-round " may, therefore, be looked upon as **varieties** *of the parental races " tall-round " and " short-wrinkled ".*

Numerous cases are known where a certain character requires the *association* of two or more distinctive factors before its effect can be seen in the offspring. Thus, Bateson found that two distinct white races of Sweet Pea (*Lathyrus odoratus*) gave, when crossed, a red-flowering variety in the F_1 generation. The two parents were pure and when self-pollinated always bred true to white; the red was only obtained when they were crossed. This at first seemed to be a case of " reversion-on-crossing " to some ancestral coloured type, but the explanation is as follows. When the red-flowering F_1 hybrid generation was selfed it gave rise in the next generation to both red and white flowers, in the ratio of nine coloured to seven white. The reason given is that the *interaction of two factors*, which Bateson called *C* and *R*, is necessary for the production of the red colour. One of the white parents is supposed to possess *C* and the other parent *R*, and as long as these factors do not come together at fertilization the progeny remains white and continues so as long as the plants are selfed. On intercrossing, however, when *C* and *R* become associated in the hybrid, the necessary condition is set up for the formation of the pigment and the F_1 generation is red. Thus, if we symbolize the parental races by *CCrr* and *ccRR*, both are white because in neither do *C* and *R* occur together. Their gametes segregate as *Cr* and *cR*, giving *CcRr* as the constitution of the F_1 hybrid, which is therefore red. The gametes of F_1 segregate in the usual way to give *CR*, *Cr*, *cR*, *cr*. If all possible combinations of these gametes are set forth as before (p. 114) on the plan of the squared board, it is found that a similar ratio is obtained, namely, nine containing both *C* and *R*, three with *c* and *R*, three with *C* and *r*, and one with *c* and *r*; but the coloured flowers are only obtained when *C* and *R* occur together, all the rest being white. Such associated factors are called *complementary*. From what has already been stated about the inheritance of colour in plants, it is clear that the factors controlling it do not appear to operate always in the same way, and Bateson's example is only one of many instances of the interaction of factors in the working of Mendelian heredity.

In the application of Mendel's principles to genetics emphasis must again be laid on the importance of concentrating upon each character separately. In actual practice, however, it is often a difficult matter to recognize the different characters in which true variation occurs.

Other forms of variation, which are better referred to as *fluctuations*, are brought about by external causes, such as change of nutrition, humidity, temperature, &c., and such forms are not inherited. Pure races, themselves homozygous, may often show fluctuation, as in height, weight of seed, &c., which might lead to the conclusion that these slight differences are heritable. Different plants of one and the same pure race may often show small fluctuations, but these conditions affect the individuals only and not their descendants.

From what has been said of the perpetuation of pure races by self-pollination, it is clear that opportunities for the creation of new varieties from such fixed types appears no longer possible. We have seen that the transmission of factors in homozygous individuals goes on unchanged, thus maintaining the constancy of features from one generation to the next. Even in pure races, however, we sometimes meet with striking abnormalities which are popularly known as " sports ". Such unusual forms may appear suddenly and are known as *mutations*. The Sweet Pea (*Lathyrus odoratus*), for instance, despite its habit of self-pollination, is known to produce variant flowers by mutation spontaneously. Such new forms, or mutants, are believed to be due to some kind of change taking place within the nucleus of a somatic or of a germ cell. The change may affect perhaps a single factor only but may communicate its effect to other factors as well. Since so much stress is laid upon the constancy of characters in the nuclei, it is conceivable that if any change occurs in those of certain somatic or of germ cells, some difference from the normal is likely to occur either in the individual (if the change is a somatic one) or in the offspring (if the gametes are affected).

Seeing that evolution could not continue if all types remain pure, the idea of *change by mutation* must be entertained if evolution is to go on, and there is little doubt that mutation does play a prominent part in producing new types, but at the present time very little appears to be known about mutations and their origin, and there is still a great deal to learn about the physical and chemical nature of genetical factors.

It may now be of interest to consider the principles of heredity after closer examination of the machinery that appears to be responsible for their working, and also to dwell incidentally upon certain kinds of nuclear changes which are worthy of consideration as playing an important part in evolutionary change and creation of new plants.

CHAPTER XII

The Mechanism of Inheritance

Vegetative reproduction ensures an exact repetition of the individual plant in all its features. Horticulturists have learnt from experience that plants grown from bulbs, corms, stem-cuttings, layering (e.g. carnations), grafting and budding (e.g. roses, apples) retain all the features of the older plants, provided they are cultivated under similar environmental conditions.

An inquiry into the probable cause of this stability of features naturally demands an examination of the mechanism of growth itself. We have seen that growth of the plant is due directly to the increase of its constituent cells, and one of the fundamental discoveries of biological science is that which connected the multiplication of cells with nuclear division. It has already been described how, during the division of the nucleus, a very precise and methodical process takes place. Here attention centres chiefly on the chromosomes; each chromosome divides longitudinally, so that at every cell-division each daughter nucleus receives an exact share of chromosome material. It is therefore inferred that the chromosomes play an important rôle in preserving the individual and integral characteristics of a plant. Though the chromosomes between successive divisions usually pass through a state of rest within the nucleus, during which they are lost to view, they are believed, nevertheless, to retain their properties unimpaired. When they appear again at the forthcoming division, they are seen to have preserved their identity, so that as far as vegetative cell-divisions are concerned, the characters of the chromosomes remain unchanged. The conclusion is drawn, and the belief is now general, that the chromosomes play a vital part in the transmission of hereditary characters.

The number of chromosomes is constant for the individual; but when reproductive cells are about to be formed this number is reduced to half. This procedure, which occurs during meiotic nuclear divisions, is essential in order to prevent a doubling of the chromosome number at fertilization. We have seen that the Reduction Phase takes place in the spore mother-cells in pollen-sac and ovule. In the early stages of meiosis, every spore mother-cell possesses two of each type of chromosome which go to make the chromosome complement of the plant, these members of a pair being called homologous chromosomes. Fundamentally, they are one paternal and one maternal, this relation having been preserved by descent from those of the fertilized ovum, despite the many somatic divisions intervening between embryo and pollen-sac or ovule. If we now designate one chromosome of a pair as A and its partner or homologue as a, a second chromosome as B with a homologue b, C with c, and so on, then the process of pairing in preparation for the heterotype division always occurs between like chromosomes, that is, Aa, Bb, Cc, &c. Again, after the heterotype division, when the two new nuclei are formed, they contain the haploid number of chromosomes—this is the essence of the heterotype division, constituting the Reduction Phase. Furthermore, a second, but homotype, division follows immediately upon the heterotype, and meiosis is then complete.

It may be of interest to consider Mendel's classical experiment of crossing tall and short peas again from the above point of view. The allelomorphic factors, T for tall and t for short, are presumably borne by two homologous chromosomes (one paternal, one maternal) in the gametes which in the hybrid F_1 generation come together as Tt. The pollen grains and ovules carry T or t in equal numbers, so that at fertilization there are four possible combinations of the factors in the second F_2 generation, namely, TT, Tt, tT, tt, or $1TT$, $2Tt$, $1tt$. The dominance of tall T over short t unites the first two combinations into 3 " talls ", so that the proportion of 3 to 1 gives the actual Mendelian ratio in the F_2 generation. The above conclusions are expressed in symbolic form in Table IV (p. 120).

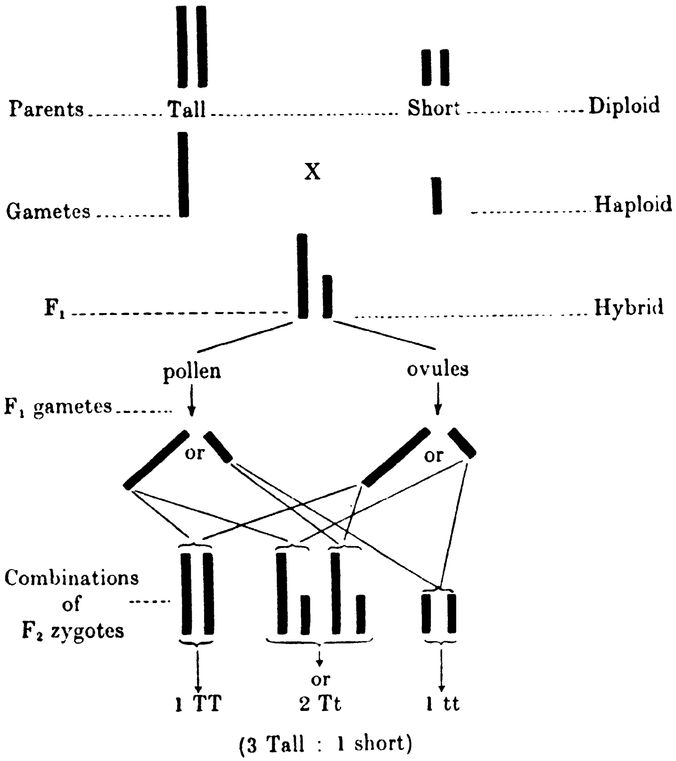
The F_2 zygotes TT and tt breed true and are therefore homozygous because their gametes carry the same factors, but in Tt, the heterozygote, the allelomorphs are together, and they will separate again, so that half the gametes are T or t.

Mendel's law of the segregation of factors in inheritance actually comes into operation during the performance of meiosis. Here, then, is a cytological interpretation of segregation and recombination of factors, supporting the view that the chromosomes are the vehicles of hereditary properties.

The average plant, in its structure and the fulfilment of its manifold functions, must obviously be controlled by a host of heritable factors. It is clear that the total number of factors is far beyond the number of chromosomes carried by a gamete and that a factor cannot monopolize a whole chromosome.

The mechanism of inheritance is easier to explain if we imagine the chromosome to consist of a definite number of bodies, which the geneticist calls **genes**. From what has been said about *characters* and *factors*, we may now say that every character is the expression of a

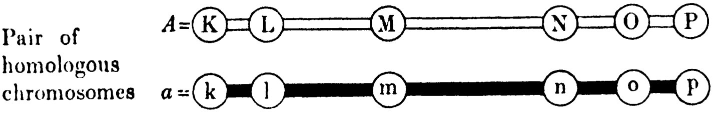
TABLE IV



pair of genes, perhaps of more than one pair. Thus, it is possible for one and the same chromosome to have separate genes to carry factors for, say, colour of the flower; shape of the petals; shape of the teeth on the margin of the leaf; number of stamens in the flower; and so on. In the same way as we have spoken of dominant and recessive factors, we may now say that one gene is dominant over the other (recessive) gene, or where some character of a hybrid is more or less intermediate in effect between those of the parents it is inferred that neither gene of a pair is capable of being fully expressed.

If we take at random any six transmissible characters, say (1) stature, (2) texture of fruit, (3) colour of flower, (4) colour of stem, (5) habit of growth, (6) shape of leaves, each of these characters would then be expressed by a *pair of genes*, namely, (1) tall and short for stature, (2) smooth and hairy for fruit, (3) purple and white for flower-colour, (4) purple and green for stem-colour, (5) upright and creeping stem for habit of growth, (6) round and oval for shape of leaf. Suppose that the genes first named, represented by the capitals *K*, *L*, *M*, *N*, *O*, *P*, respectively, are dominant and that the second, related genes symbolized by the corresponding small letters, *k*, *l*, *m*, *n*, *o*, *p*, are recessive. If these genes are now arranged as particles in parallel series along two lines representing homologous chromosomes, called *A* and *a*, the dominant genes being in *A* and the recessive genes in *a*, then the process of pairing at meiosis, preparatory to gamete formation, may be represented thus:—

TABLE V



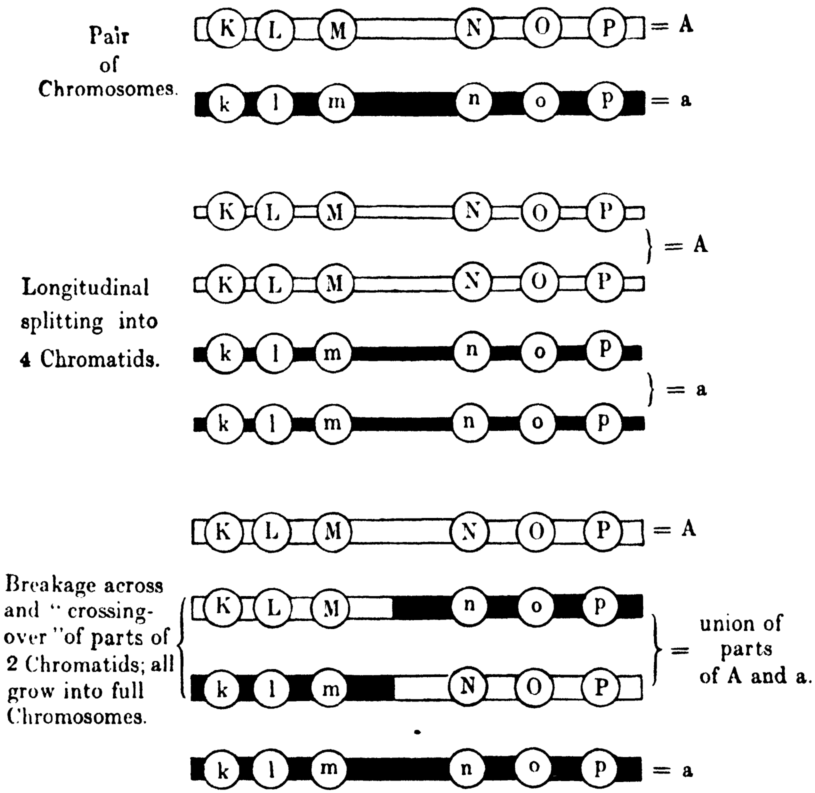
In the diagram, stature is expressed as *K*—*k*, tallness in *K* and shortness in the opposite allelomorphic gene *k*. The dominance of *K*, *L*, &c., in their impress upon the plant does not mean that the recessive genes *k*, *l*, &c., are without significance. Although we shall return to the topic again, it may be stated incidentally that one view of the origin of mutations, discussed briefly in the previous chapter, is that they result from internal changes which may take place within, perhaps, a single gene. To explain the feasibility of internal changes taking place within a gene, it is surmised that a gene, instead of being a simple particle, is itself of compound structure. If the ultimate bodies within a gene are capable of rearrangement, the change, though in itself trivial, may have considerable effect on the general genetic constitution of the plant. Nothing, however, is known of the ultimate structure of a gene, but, whatever its nature, as part of a chromosome, it is capable of growth and division, and we can understand that if any alteration takes place within a gene, it will inevitably be reflected by some change in the factor expression. This is what we understand by *gene mutation.*

If we revert to the sequence of events at meiosis when pairing of homologous chromosomes takes place (Ch. V, p. 67), each chromosome splits into two halves or chromatids, so that a chromosome-pair now consists of four chromatids lying parallel and in close association, the genes, as represented above, occupying corresponding positions, the dominant genes on one chromosome directly facing the recessive genes on the other.

It is necessary now to go somewhat further into the question of

" crossing-over " already mentioned in connection with the formation of the germ cells (Chap. V). According to the gene theory of chromosome structure, pairing of homologous chromosomes may be represented as follows (see also fig. 26):

TABLE VI


Pair of Chromosomes.
K L M N O P = A
k l m n o p = a
Longitudinal splitting into 4 Chromatids.
K L M N O P
K L M N O P
= A
k l m n o p
k l m n o p
= a
Breakage across and " crossing-over "of parts of 2 Chromatids; all grow into full Chromosomes.
K L M N O P = A
K L M n o p
k l m N O P
= union of parts of A and a.
k l m n o p = a

The allelomorphic genes are again represented by *Kk*, *Ll*, *Mm*, *Nn*, *Oo*, *Pp*, and they occupy definite though not necessarily equidistant points in the chromosomes; thus *KL*, *kl* are closer together than *MN*, *mn*, and so on. This relative closeness of the genes has an important bearing on " crossing-over " and is discussed below.

If the chromosomes, at pairing, did nothing more than divide evenly as shown in the middle group of the above figure, the gametes would always be of two kinds with the same series of genes. As the result of crossing-over (here illustrated very simply indeed), however, it is believed that two of the chromatids, one from *A* and one from *a*, break across and that the broken ends of different chromatids join together to form new chromatids. All four chromatids eventually grow to the size of full chromosomes. Of the four resulting chromosomes, therefore, two are like those of the respective parental type, and two, which are now reconstituted chromosomes, share the parental factors. The four chromosomes segregate at gamete formation. Thus when they finally enter the pollen tetrad (the same occurs in the ovule tetrad), if we adopt the above convention of " black " and " white " for the homologous chromosomes, one pollen grain will have a " white " chromosome; one a " black " chromosome; and two will each have a chromosome "part-white" and "part-black". Moreover, in the "part-coloured " chromosomes the *genetic constitution in terms of dominants and recessives is different* from that in either of the parental chromosomes. This rearrangement is due to crossing-over and exchange of segments. (See also fig. 26.)

From what has been said above of the relative proximity of the genes, it follows that breakage and crossing-over is more likely to take place at a point or points (there may be more than one cross-over) where the genes are far apart than where they are close together. Thus it would almost invariably occur that *KL* and *kl* would find themselves together despite an exchange of segments, but that *MN* and *mn*, being much farther apart, would, after crossing-over, have exchanged into different chromosomes. The likelihood is that the genes *K*, *L* and *k*, *l* will remain together on the same chromosome or segment, and accordingly when selfing takes place, for instance, in the F_1 generation, the offspring will inherit in like degree those features of the plant with which the factors *K*, *L* and *k*, *l* are concerned. Genes which thus remain together despite one or more cross-overs are known as *linked* genes.

As the result of crossing-over, the chromosomes emerge from this stage in an altered condition, to the extent that, as stated above, some of the chromatids have exchanged one or more portions of their length according to the number of cross-overs which took place. *These opportunities, presented in pairing at meiosis, whereby chromosomes may be reconstituted, form the basic principle of plant breeding, and crossing-over presumably involves a mechanism whereby the genes are combined and recombined in many ways.* Some of the pollen grains and ovules of a species may, therefore, be genetically different from those of the parent plants because the relative arrangement of genes in their chromosomes is different. When such gametes of altered constitution come together at fertilization the zygotes are endowed with new combinations of hereditary factors. Such new formations are bound to be reflected in possibly new morphological or physiological features. In other words, crossing-over appears to be a means whereby variations may arise and on which natural selection can exert itself.

We have hitherto been concerned with the conditions of diploidy and haploidy in nuclear structure, the former showing the nuclei with two of each type of chromosome in the somatic cells ($2n$), and the latter condition, present in the gametes (n), having only one of each kind, the separation of the members of a pair having occurred at meiosis.

Although the chromosome number is constant and characteristic of a species, numerous instances are known of plants which possess more than two of each kind in their chromosome sets. This multiple condition is known as *polyploidy*. A classical example of a polyploid plant is the Chinese Primrose (*Primula sinensis*). This plant exists in two hardly distinguishable forms, but one of them contains 24 chromosomes and the other 48 chromosomes in the nuclei of its somatic cells (diploid).

Since the normal plant is usually called the diploid, because it has double the gametic number of chromosomes, the term *tetraploid* is applied to the new form of *Primula*, because its somatic number is four times that of the basic gametic number of 12 in the original species. The new *Primula* is therefore furnished with four of each kind of chromosome instead of two as in the diploid and is accordingly called a *tetraploid* type. Other plants of polyploid constitution may have the basic haploid number of chromosomes repeated three (triploid), five (pentaploid), six (hexaploid), seven (heptaploid), eight (octoploid) times, &c.

When a polyploid type proceeds to form its gametes, the passage through meiosis is not nearly as exact and smooth in its working as in diploid plants. In the tetraploid Chinese Primrose, for instance, where one would expect the 48 chromosomes to be arranged at metaphase in 12 groups of four (quadrivalents), this is not usually the case; in some of the spore mother-cells, presumably according to chance, they may arrange themselves on the spindle in twos (bivalents), threes (trivalents), and fours (quadrivalents). These irregularities at polyploid meiosis are important, for they naturally interfere with the exact sharing of chromosome material into the gametes. If the 48 chromosomes were to form 12 quadrivalents and each quadrivalent were to behave like a normal bivalent by sending half its number of chromosomes to one pole and half to the other pole of the spindle, then meiosis would be regular; but sometimes three may go together to one pole, leaving only one to go to the other. In this way some gametes would come to possess a surplus and others a deficiency of chromosomes. These irregularities of distribution of hereditary substance into the gametes often render them ineffective as sexual cells, so that the flowers of polyploid plants are frequently sterile and incapable of setting seed.

Polyploidy may arise in two ways. It may occur either at somatic division in the plant body or within the spore mother-cells. In the former case, a diploid plant may produce from no apparent cause one or more branches which are, say, tetraploid in their nuclear structure. Such branches may not show any marked morphological differences from the normal, and they arise from buds which originate in the usual way from single cells in which, however, the chromosome complement is double the normal number. This duplicate condition may come about by *suppression of the cross wall* between the two chromosome-sets formed at the first division of the initial cell of the bud. If the cell possesses, say, 14 chromosomes, dividing in the usual way to form two sets of 14, instead of these being separated by a cross wall, they remain in the initial cell and reassemble into a nucleus of 28 chromosomes. This cell will divide as one normally containing 28 chromosomes and give rise to a tetraploid branch. The phenomenon is known as *somatic doubling.*

Polyploid branches may arise in the above manner spontaneously, but they can also be produced in certain diploid plants as a result of injury or pruning. In the Tomato plant ($2n = 24$) tetraploid branches may be developed by cutting away the tips of young vigorous plants; some of the new branches arising from the callus-tissue which covers the wounds are seen to differ from the rest of the plant in such features as thickness of stem and character of foliage. The cells of the new shoots show not 24 chromosomes but 48, that is, they are tetraploid. A shoot of this kind takes its origin from a single cell of the regenerating callus-tissue which at division passed through the same nuclear changes as described above for somatic doubling. Moreover, the tetraploid shoots of the Tomato can be removed from the parent plant and propagated vegetatively; they may actually produce flowers and fruits. Sexually, however, the tetraploid plants are not so fertile as the diploid, but owing presumably to their increased chromosome-content they are capable of *wider variation* than the diploid forms. This may be seen in a greater variety of colour in the tomato fruit and in increased activity of certain physiological properties of this plant.

Polyploidy may also have a sexual origin; it may arise from the fusion of sexual cells which have failed to negotiate the reduction phase. This irregularity arises in the spore mother-cell, and may be traced to a breakdown at the heterotype stage of meiosis. Instead of the bivalent chromosomes in the mother-cell separating normally at metaphase, sending an equal number of chromosomes to each pole of the spindle to form the two nuclei of the heterotype division, they make but a feeble attempt at segregating, only to come together again in irregular fashion in the mother-cell; they will, however, divide by ordinary mitosis. In other words, a spore mother-cell omits meiosis altogether, and its nucleus divides successfully only once. A pollen grain, or ovum in the ovule, derived in this way thus comes to possess twice the number of chromosomes characteristic of normal gametes; they are of the same chromosome number as somatic cells and are, therefore, diploid or *unreduced gametes.* When such gametes meet at fertilization the resulting zygotes are tetraploid. The tetraploid plants derived by this method are only different from their diploid parents in that they have each type of chromosome repeated four times instead of twice. The phenomenon of tetraploidy may therefore be accounted for either by the incidence of " somatic doubling " or by the fusion of " unreduced gametes ".

Polyploids may also arise as hybrids, that is to say, as the result of a cross. This can be illustrated by the classical example of crossing the Radish plant (*Raphanus sativus*) with the Cabbage (*Brassica oleracea*). The crossing is not reciprocal and the Cabbage is effective only as the pollinating parent. Although these plants both belong to the *Cruciferæ* family, they are not considered to be very closely related, as they are species belonging to different genera. The somatic number of chromosomes in both plants is 18 ($2n$), and the gametic number is 9 (n). Though they are of distinct genera, a " cross " is successfully performed; the F_1 hybrid is more or less intermediate between the parents in its morphological features. It is almost sterile but not completely so, and a few seeds are produced. The somatic number in the F_1 hybrid is also 18, derived in the usual way, 9 from each parent. When, however, the hybrid proceeds to form its gametes all manner of irregularities arise, as the 18 chromosomes are unable to sort themselves into homologous pairs. Without actually establishing 9 bivalents at metaphase (the chromosomes are " too different " for this), the 18 univalents separate in all sorts of uneven combinations, say 11 to one pole and 7 to the other, so that when the gametes in pollen and ovule are formed fertilization between them obviously fails because of the dissimilarity in kind and number. Presumably from pure chance, however, some of the spore mother-cells pass through the history of the " unreduced gamete ", mentioned above. The result is that some gametes come to possess the full complement of 18 chromosomes from ordinary mitosis of the number in the mother-cell. Actually, the mother-cell divides only once to form two cells each containing 18 chromosomes, 9 of which are Radish chromosomes and 9 Cabbage chromosomes. Each gamete is then certain to have all the chromosomes of both parents. When such unreduced diploid gametes in pollen and ovule meet in fertilization the chromosomes are now able to pair and tetraploid seeds ($2n = 36$) are formed. Such is the history of the few seeds obtained in the F_1 hybrid generation. They give rise to tetraploid plants (intermediate in character between the two parents) in which meiosis is regular, the gametes are fertile, and the progeny breeds true.

Under natural conditions it is believed that such polyploids appear spontaneously as the result of chance hybridization and that, despite a considerable degree of sterility in the hybrids, continuance of the race depends upon a chance seed or seeds being formed as the result of the fortuitous union of unreduced gametes. The seeds though few and rare produce perfectly fertile offspring, and if they respond successfully to their environment they may originate a new type.

It is significant that a great measure of sterility exists among plants which exhibit deviations from the normal diploid condition of their chromosome complements. We have seen that these aberrations ultimately affect the constitution of the gametes, and were it not for the incidence of somatic-doubling or the fortuitous intrusion of unreduced gametes into the life-cycle, such new forms could not be perpetuated sexually.

The production of hybrids, though they are so frequently sterile, is, however, of great practical importance to the horticulturist, who is concerned perhaps less with the future fertility of his plants than with their retention in cultivation. This he is able to do by resorting to vegetative means of propagation, and there are comparatively few garden, orchard, or ornamental plants that cannot be perpetuated by some kind of asexual means. Some species of Tulips, Hyacinths, &c., and a large number of flowering ornamental shrubs are so highly sterile that they can be continued only by vegetative means. The same applies to practically all our fruit trees, and though the actual fruits are the products of fertilization, the contained seeds are often highly infertile. Nearly all our varieties of apples, pears and plums, for instance, depend for their continuance on the grower's success with " budding ", " grafting ", &c.

Though the incapacity of many hybrids to form seeds is due largely to discrepancies at pairing of dissimilar chromosomes in gamete formation, the two sets derived from the respective parents are apparently able to co-operate as long as their relations are purely somatic, that is, as long as these hybrids are cultivated vegetatively. It is at the reproductive phase that difficulties are encountered. We have indicated, in a few cases, the means whereby such difficulties may be surmounted. It does not always follow that as the result of a few experiments in crossing of species, failure of the hybrids to set seed is a certain criterion of complete sterility; experimentation should be protracted and on a wide scale. We are still unaware of the natural conditions which are responsible for these chance phenomena, and seed formation by polyploidy is so precarious as frequently to demand long and tedious trials. Yet some of the most important newer races of economic plants now grown on a wide scale are the descendants of but a few hybrid seeds obtained from single plants (Chap. XIII).

It is known that certain species will not form hybrids at all. Failure to do this is caused by too great a disparity in number and quality of the respective chromosomes; the numerical difference may be too great to attempt even a somatic association. Instances are known of triploid plants being obtained by crossing diploids and tetraploids, but triploids and other odd-number polyploids are highly infertile. The production of fertile hybrids between varieties of the same species or between closely allied species is feasible owing to a resemblance in number and quality between their chromosome complements. Other attempts at crossing of species, even of those within the same genus, are often futile. In general, the more distant the relationship between the plants concerned, the fewer chances there are of obtaining fertile hybrids.

Before we pass on to the economic aspects of plant hybridization it may be of advantage to review the problems of heredity in the light of the chromosome theory. Plants produced by vegetative propagation preserve their characters unchanged because their chromosomes divide evenly, thus ensuring complete identity of the genes; apart from modifications due possibly to environmental change or methods of cultivation (or, rarely, somatic mutation), they are always the same. Again, sexual reproduction is unhampered as long as chromosomes are homologous and meiosis is regular. Mendel's pure races of the edible pea retain their homozygosity as long as they are selfed. When the different races of this species are crossed, the chromosomes of different parents, half the number from each, meet in fertilization, and although they are similar they are not identical; hence heterozygous forms arise as well as homozygous forms. Further, the phenomenon of crossing-over brings in its train possibilities of chromosomal exchange, culminating in some of the gametes being endowed with hereditary material different from that of the parental gametes. The occurrence of linkage, again, despite segmental crossing, ensures that some at least of the parental factors appear together in the offspring. The crossing of closely related species is practicable provided the chromosomes are equal in number, a fact which can often be shown cytologically. When difficulties arise in the crossing of other species, the microscope may reveal a divergence in chromosome number. When, sometimes, these difficulties are surmounted, cytological examination may show that the chromosomes have duplicated their number, with the result that fertile polyploid plants are formed.

A general comparison of diploid and polyploid plants gives a strong impression that the possibilities for variation are greater in the latter than in the former. Polyploid types seem to have greater capacity for the production of small gradations in certain characters than is usual in diploid plants. Where in the diploid, for instance, one gene controlling the factor, say, for " hairiness " is definitely dominant over " smoothness " in its allelomorph, in the polyploid form of the same plant this clear distinction may not be evident; on the contrary, there may be considerable intergrading in respect of hairiness and smoothness. The reason appears to be that dominance can be fully exercised only when there are two chromosomes of a kind (diploid); when a chromosome occurs four or more times over, an element of indecision in factor control appears to be introduced, so that dominance is subject to competition among the genes and accordingly no factor is capable of showing its full expression. Such intergrading of factor-effects is common among polyploids. A considerable body of information is gradually accumulating in genetical work with both diploid and polyploid plants, to the effect that factors are not so isolated in their effects, but that a great deal of interaction exists among the genes. Crane and Lawrence, working on the genetics of the highly variable Garden Dahlia (*Dahlia variabilis*), an octoploid species, point out that this plant exhibits an extensive array of colour shades. These authors state that the pigmentation is controlled not only by individual genes, some intensifying, some diluting, and others inhibiting in their effects, but by the *total* number and proportion of all the colour-controlling genes.

Clearly, then, a case has been established that the mechanism of inheritance lies in the chromosome or more definitely in the gene. Darlington[1] sums up the evidence in favour of the chromosome theory of inheritance very clearly: " Mendel imagined corresponding pairs of factors in the plant; now, corresponding pairs of chromosomes are found in all its cells. He imagined the segregation of factors in the production of cells; now, the separation of chromosomes is seen. He imagined the recombination of corresponding factors at fertilization; the cytologist sees the two groups of corresponding chromosomes unite. . . . Even where the application of the laws of Mendelism is complicated or modified out of all direct recognition, nevertheless it is known that the same principles must be at work because the same kind of mechanism is observed."

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[1] Darlington, C. D., *Chromosomes and Plant Breeding*, p. 26 (Macmillan).

CHAPTER XIII

Hybridization and Improvement of Cultivated Plants

The improvement of cultivated plants by selection and hybridization is of comparatively recent origin. Up to the beginning of the present century attention was bestowed almost entirely on the selection of individual plants from a mixed population, and these were submitted to various and possibly better methods of cultivation. The interested grower would keep on choosing the individuals showing the desired features, and if his selected plants were of the kind that could be multiplied by asexual means there was every likelihood that the improved forms could be maintained by vegetative propagation. Moreover, experience had taught him that such improved types had a tendency to revert to their original form if they were not continually selected and cultivated under the most favourable conditions. If the type was capable of propagation by seed, there would perhaps be some measure of disappointment if the majority of the plants produced still showed many of the undesired characteristics of the ancestral type. The grower's method of selection and cultivation had evidently gone far to improve the individual without, however, improving the race.

By dint of continued selection, of harvesting and sowing the seeds produced, however, he found that some of the progeny, only a few perhaps, turned out to be true to the characters of their immediate parents. This was a great step forward, for if these features could be continued unimpaired from one generation to another by seed, the grower had arrived, by mere chance, at a particular " strain " which might be called a *pure line.* We know that such a strain must have emanated from a race in which both cross-pollination and self-pollination were effective, for the wide range in variation responsible in the first instance for the mixed population must have come about through mutations, their spread through the population and the selection of the fitter combinations of genes. If, however, variation is to be limited in its scope, self-pollination or cross-pollination between individuals of similar gametic constitution (in-breeding) is essential. But the mysteries attendant upon promiscuous pollination had barely been realized in the early days of plant improvement, and it would inevitably follow that pure lines could be improved no further, since their progeny from selfing (or in-breeding) would be in possession of the same heritable factors as their parents and attempts at further selection would be impossible.

One must not, however, ignore the fact that a great measure of advance in the improvement of plants was, and is still being, maintained in this way; hybridization controlled by the plant breeder is only resorted to when selection alone fails to produce the desired results.

The difficulties attendant upon the growth of plants under cultivation are apparent to everyone. They are the inevitable outcome of man's interference with the delicate balance existing between plants growing under natural competition. In no instance are the difficulties greater than in the development of agriculture in the tropics, where the clearing of natural growth has been replaced by the planting of economic crops. Here, natural selection has been forced to give way to human selection, and the harmonious existence of the native vegetation, rich in variety, has been disturbed by the introduction of species foreign to the environment. The immediate result of the changed conditions is that the new crops almost invariably fall prey to epidemic diseases. Accordingly, in the first instance comes the need of combating disease, for cultivated plants when crowded together in crop formation are far more liable to the attacks of fungi, insects and micro-organisms than their progenitors in open nature. Diseases like " Potato-blight " and the various forms of " Rusts " which attack cereal crops spread very rapidly once they make their appearance. Economic plants are often grown under such intensive cultivation with a view to increasing the yield, the bulk and succulence of vegetable or fruit, &c., that they are rendered highly susceptible to disease. Intensive cultivation, in all its aspects, tends to alter the constitution of the plant in such a way that if the improved forms were to return to open competition under natural conditions, the probability is that they would never survive.

Unlike animal diseases, plant maladies in general do not submit to curative treatment, and in but a few cases, and only in the early stages of attack, are preventive measures of any value. While much can be done to combat plant diseases by methods of clean cultivation and timely application of fungicides or insecticides, it is to the geneticist and plant breeder that the grower must look for help in the control and prevention of disease. The need is real, especially in the practice of agriculture and the cultivation of economic plants in the tropics, for the annual losses due to the ravages of disease caused by insects, fungi, bacteria, and to the insidious types of " virus " diseases (in which no causal organism can be visibly demonstrated), are enormous.

The rediscovery of Mendel's Principles of Heredity in 1900 gave a great impetus to experimental hybridization. If clear-cut characters such as height of stem, shape of seed, colour of cotyledons, &c., with which Mendel experimented, were found to be governed by heritable factors, would genetical analysis also reveal independent inheritance of such features as disease resistance and susceptibility to disease, of yield, of time-of-maturation, of chemical plant-composition, &c., and could these factors be controlled by hybridization? If, for instance, the mode of inheritance of susceptibility or immunity in the case of a disease could be determined, there would possibly be scope for experimentation on the lines of combining disease resistance with other desirable characters. It is at this point that the geneticist comes to the aid of the pathologist, and to-day new varieties of all kinds of economic plants have been developed, which have attained in some cases high degrees of resistance, and in others complete immunity from specific diseases, while at the same time the new types are in possession of the desirable characters of the original stock.

The breeding of disease-resistant varieties is, however, greatly hampered by the occurrence of variation among the parasitic organisms themselves, and it is becoming more and more apparent that disease organisms are constantly exhibiting distinctive physiological races. Thus the parasite *Puccinia graminis*, which causes Black Rust of Wheat, occurs in numerous forms which vary considerably in their powers of infection; a certain variety of wheat may be resistant to some of these forms but not to all of them. Moreover, these physiological races differ in their infective properties according to the locality of the host, so that in the breeding of resistant varieties the occurrence of distinctive strains of one and the same organism of disease is very troublesome. It follows that such work must be carried out with a view to the building up of a new type that will not only be resistant to a certain parasite but to a particular strain of that parasite, and the conditions of the environment must also be taken into account.

One of the earliest investigations, in this country, into the problem of hybridization in relation to the breeding of resistant host varieties was that of Professor Sir Rowland Biffen on wheat. Not only were varieties of this cereal found showing variations in the extent of resistance to Yellow Rust (*Puccinia glumarum*)—which in this country is more of a menace to wheat than the Black Rust (*P. graminis*)—but after careful selection, a kind highly susceptible but otherwise desirable was crossed with another kind which though of inferior quality showed itself to be immune from this rust. While we cannot here give details of Sir Rowland Biffen's outstanding work on the improvement of wheat, it should be mentioned that he was finally able to combine rust-resistance and greater yield of grain with other valuable characters, in one variety.

Genetical analysis, again, has brought to light the important facts that other features, such as the duration of the growing period, quality of endosperm, drought resistance, &c., can also be controlled by judicious selection and hybridization. It is now possible to obtain strains of wheat (and of other cereals) which come to maturity appreciably in advance of the older types, and in colder latitudes, where the length of the growing season is comparatively short, this feature is obviously of the greatest value. Moreover, early maturing strains are valuable from another point of view, for their early ripening often enables them to escape disease. Whilst such forms, otherwise valuable, are not actually resistant to " rust ", they are, nevertheless, able to escape an attack, because the grain is mature before the disease makes headway.

Hybridization has also played a very important part in improving the quality of the wheat grain, that is, in the nature of its endosperm. Whereas most of the older types of wheat were of the soft or " mealy " texture of endosperm (fig. 35), difficult to pulverize in the milling processes and giving on the whole an inferior type of flour and a " heavy " bread, nearly all of the new wheats are of the hard or " brittle " type which respond to greater fineness in the milling technique and with better baking properties give altogether a greatly superior kind of bread.

Heavy losses of crops due to drought are now obviated by the introduction of new strains developed expressly for the purpose of tolerating prolonged periods of dryness. Notwithstanding all these successes, however, it is imperative that all improvements resulting from plant-hybridization must be considered in relation to the environment. It is one thing to build up a hereditary assemblage of factors which are in harmony with a particular type of climate and soil and another to expect the same strain of plant to respond favourably to a totally different environment. It must be borne in mind that the living plant is a highly elaborate and delicately balanced piece of machinery controlled by innumerable genes. The genes not only interact to produce the characters for which they are responsible, but they are only fully efficient in their character control when in complete accord with the environment.

We have thus far indicated briefly the trend of improvements as illustrated by the most important of our food plants, namely, wheat. The story is much the same for other economic plants, such as oats, maize, potatoes, pasture grasses and clovers, cotton and jute, vegetables, fruit, &c. The aims in view are similar, namely, greater yield, better quality, and capacity to resist disease.

Stations and institutions whose work is concerned with genetics and plant breeding are now established in many part of the globe. In Britain priority of place must be given to the John Innes Horticultural Institution, Merton, specializing in the study of experimental genetics; and the plant breeding stations, in England, at Cambridge; in Scotland, at Edinburgh; and in Wales, at Aberystwyth.

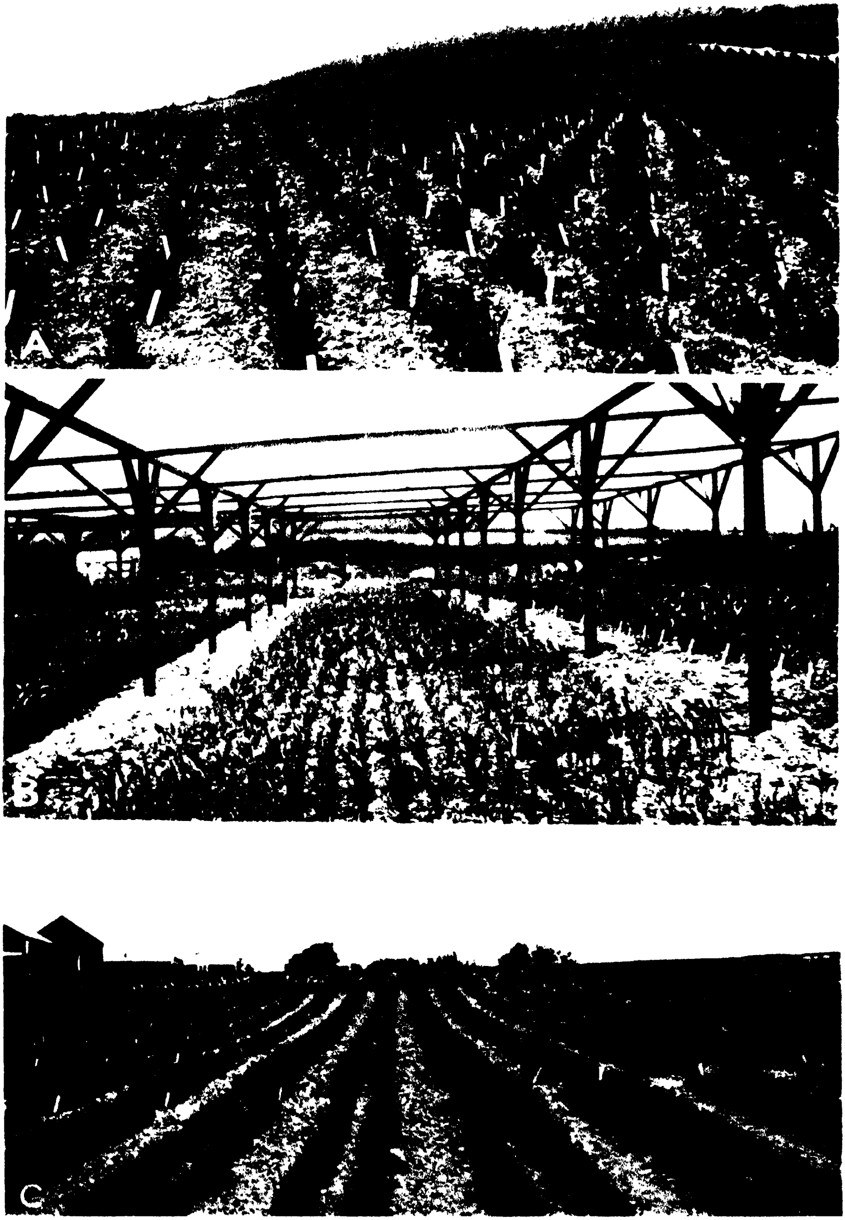
By the courtesy of Professor Sir George Stapledon the writer is privileged to give a brief account of the work and of the technique employed at the Welsh Plant Breeding Station. Improvement here is concerned mainly with herbage plants, namely, grasses and clovers; with genetics and practical breeding of oats and wheat, together with investigations into plant diseases. The wide scope of experimentation may be realized when it is stated that in one year (1933) in connexion with genetical researches and practical breeding with grasses and clovers, together with the work in progress on plant diseases and other problems, no fewer than 443,200 seeds and seedlings were dealt with.

At the outset the investigator has to acquaint himself with everything there is to know about the crop which he wishes to improve, and in what directions and for what purposes improvement is needed, and only then is he competent to explore the fields of genetics and cytology with any reasonable hope of harnessing these sciences to his purpose.

The first necessity is to assemble as large and as representative a collection of living plants of the species under study as possible. Plants collected from all parts of the world, from more or less natural habitats, are in as great demand as those from ordinary commercial sources. On examining and classifying all this wealth of material, one is struck with the *wide range of variation* within every species. Thus, Perennial Rye-Grass is not just Perennial Rye-Grass, nor is White Clover just White Clover. Each species consists of innumerable *races* and *forms*.

At the Welsh station improvement in herbage plants is achieved by three distinct methods of procedure. There is firstly the finding and standardization of highly desirable regional strains. The next stage is to endeavour to improve such strains by " type concentration ", that is, by a method designed to increase the concentration of the most desirable forms of plants and to decrease the less desirable within the strain. Though much might be said about the achievements of the station along these lines, the present account is chiefly concerned with the improvement adopted in the third stage. This is to proceed by strictly genetical methods, employing artificial hybridization and progeny tests at all stages.

In the case of the grasses, for instance the Perennial Rye-Grass, inflorescences which are to provide pollen for a " cross " are " bagged-up " a few days before they are expected to commence flowering, the bags used for this purpose being made of thin glazed transparent paper.



Welsh Plant Breeding Station, Aberystwyth

A. Generations of oat plants (F_3 to F_7), in rows in the field, for selection and "fixation" of desirable new strains.

B. The F_2 generation of an oat "cross", in a bird-proof cage; for study as spaced single plants.

C. Multiplication of "fixed" strains, in F_8, to provide initial seed for testing relative yields.

The stems just below the inflorescences are embedded in cotton wool, the bag is brought over the inflorescence and its mouth lightly tied over the wool with raffia, thus affording protection against any external pollen. The pollen collects in the creases of the paper bag and can be extracted with little or no loss. The next step is the removal of the stamens from the spikelets, in preparation for cross-pollination by hand. This mutilation of the spikelets does not seriously interfere with seed-setting. With the use of a very soft brush, the pollen is well distributed over the inflorescences of the female unit; all these operations are carried out in a draught-proof greenhouse. (See plate facing p. 136.)

There is a wide range in the flowering-times (i.e. the exsertion of anthers) of the different types of grasses. It is interesting to note that under normally favourable weather conditions the tendency is for different species to shed their pollen at different and particular hours of the day. A considerable number of grasses shed pollen only in the morning: thus *Lolium perenne*, from 9 a.m. to 11 a.m.; *Festuca rubra*, from 9.45 a.m. to 2.30 p.m.; *Alopecurus pratensis*, from 6 a.m. to 7.45 a.m.; *Phalaris arundinacea*, from 5 a.m. to 10.15 a.m.

Sometimes it is desired to carry out hybridization between plants which do not flower at the same time. They may be caused to flower together by delaying the flowering date of the earlier-flowering plant. The method consists in controlling the length of exposure of the plants to daylight; the plants are placed on trolleys and wheeled in and out between a light-proof house and the open. This method has been successfully used e.g. in causing early-flowering races of the Cocksfoot Grass (*Dactylis glomerata*) to flower at the same time as the later-flowering kinds.

The technique of the artifical pollination of clovers is interesting. With the clovers, which are largely self-sterile, removal of the stamens is not necessary, and pollination can be effected at any time of the day. For the building up of new strains by inter-reciprocal crossing, bees are used. The plants for inter-pollination are set out in bee-proof compartments in a large greenhouse specially constructed for the purpose. For Red Clover the most suitable species of bees to use are *Bombus hortorum* and *B. agrorum*, and for White Clover, *B. terrestris*. These species are caught in sufficient numbers when visiting decoy plants of Larkspur (*Delphinium*) which are maintained near the hybridizing house. The bees are washed by gentle agitation in wide tubes containing tepid water, in order to remove or destroy any pollen of Red Clover which they may happen to carry. To render any adhering pollen completely ineffective the bees are carefully dried, after which they are ready to be introduced into a compartment, where by passing from flower to flower they effect the necessary reciprocal pollinations.

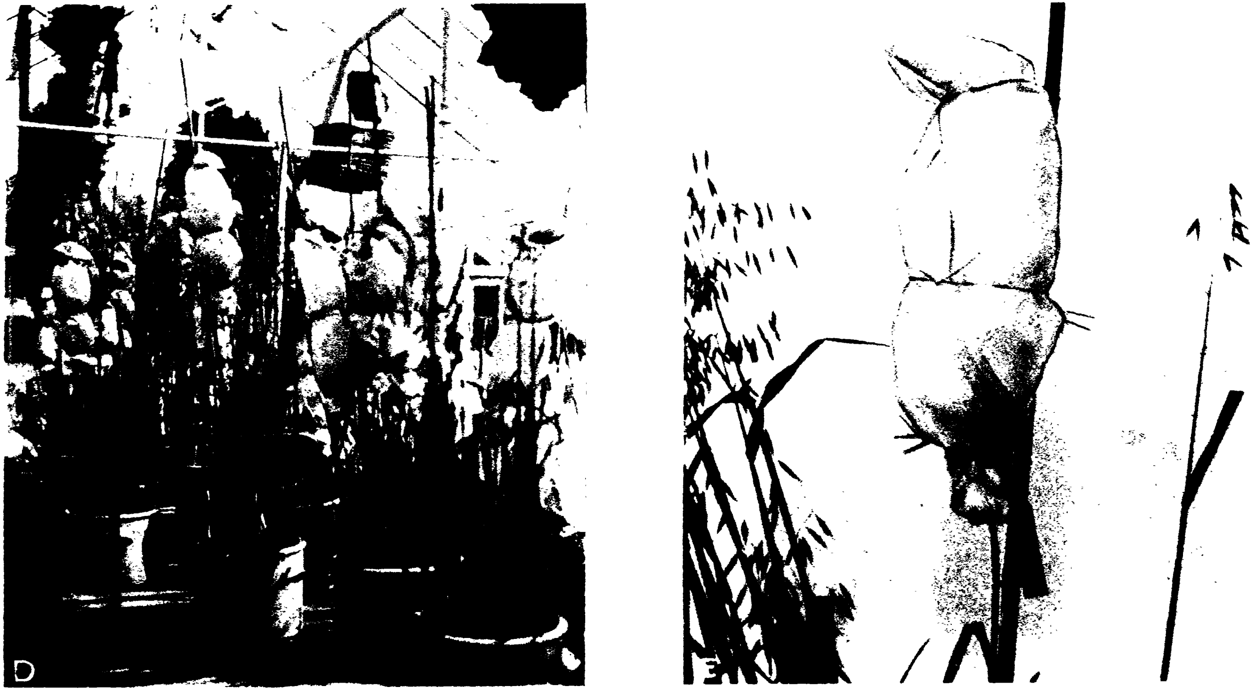
The procedure with Oats follows much the same lines as that for the Grasses. It is generally assumed that the Oat is essentially self-fertile, but recent studies have revealed the fact that when different varieties are grown close together there may be natural crossing to the extent of about 10 per cent. The actual plant breeding with Oats follows two main directions, namely, the selection of pure lines and the production of new varieties by hybridization. It is worthy of note that a considerable measure of success has been attained by *wide* crosses between different species of Oats, with a view to combining such valuable features as standing-ability of the straw with quality of the grain and yield, and resistance to Rust diseases.

In the hybridization of Grasses, crosses have been obtained between Rye-Grass and Fescue, *Lolium perenne* and *Festuca elatior*, var. *arundinacea*, and between *F. elatior*, var. *pratensis* and *Lolium perenne*. From these wide crosses between Rye-grasses and Fescues a wide variety of divergent plant types have been produced, some of them cytologically very abnormal. Professor Stapledon indicates a point of extreme interest and importance, namely, that the material is exactly of the character from which new types may be expected to arise by the *doubling of the chromosomes*.

In actual practice the work of the plant breeder is beset with numerous difficulties. We have already indicated that the production of strains for resistance to specific diseases often renders the new forms susceptible to other diseases and that parasitic organisms themselves are also open to evolutionary change with production of biological forms.

The incidence of linkage, again, is often greatly disconcerting in the crossing of forms when it is desired to segregate certain factors. Thus in the case of Potato Blight (*Phytophthora infestans*), some of the best varieties of potatoes are extremely susceptible, and unfortunately there appears to be a close linkage between the quality factor and susceptibility which is difficult to break. Again, the Rusts are serious diseases of the cereals and, for instance, in the breeding of a variety of Oat immune to the ravages of Crown Rust (*Puccinia coronata*), there seems to be strong linkage between resistance and undesirable quality of the grain.

Another difficulty arises in relation to self- and cross-pollination in respect of *heterosis* or *hybrid vigour*. As a rule it may be stated that the practice of selfing plants which are normally cross-fertilized leads to diminishing vigour in the progeny, but that in other types which possess a high degree of self-fertility the effects of in-breeding are not so serious. Professor Stapledon reports that the great majority of the perennial grasses and clovers are essentially cross-fertile, a few species, however, having a high degree of self-fertility. Red and White Clover, the former species to the greater extent, are highly though not abso-



Welsh Plant Breeding Station, Aberystwyth

D. Selected oat plants for hand crossing, growing in pots in a cool greenhouse.

E. *Right:* A single oat panicle with lower spikelets removed, in preparation for removal of stamens and pollination—only six florets are usually retained for pollination. *Centre:* a pollinated panicle protected with a pollen-proof bag after completion of pollination.

(By courtesy of Professor Sir George Stapledon and Mr. E. T. Jones, Aberystwyth.)

lutely self-sterile, but the majority of the herbage plants of agricultural usefulness in this country are essentially cross-fertile species. It follows that the effects of in-breeding in all its degrees of intensity have to be critically studied for each species upon which improvement work is undertaken. The tendency is for selfing and the crossing of individuals of the same progeny to lead to loss of vigour, and the procedure is frequently accompanied by the appearance of abnormalities. These take the form of inherited characteristics which in some way or another inhibit normal robust and vigorous growth. The responsible factors are deemed to be *lethal* and are manifested, for instance, in chlorophyll deficiency and in various types of dwarfness and malformation. In practice, therefore, it is obviously of the highest importance to limit the effects of selfing and in-breeding by controlling pollination.

At the Welsh station the method adopted in order to maintain heterosis and vigour in plants of normal cross-pollinating habits is to build up " single " plant lines, at once highly vigorous and attractive from the agricultural point of view, and to maintain them in subsequent generations by allowing them to inter-pollinate freely. As long as they are ensured of a measure of isolation from other similar crops, their purity, even in the case of the wind-pollinated grasses, can be maintained if mass-flowering and continuous production of flowers can be established. An endeavour is always made, therefore, to start with as large areas as possible in the field, and to isolate such areas from alien strains of the same species. In the case of Clovers, for instance, profusion of flowering is a very effective means of avoiding contamination for the simple reason that a mass of flowers tends to hold the bees to a particular area.

Another method of controlling pollination with a view to the maintenance of vigour, while at the same time preserving the purity of the strain, may be illustrated by work done in America on the Maize (*Zea Mays*). This plant bears its staminate and carpellary flowers in different inflorescences on the same individual. It is a plant well adapted for wind pollination; the staminate flowers form a loose panicle, and the feathery stigmas of the carpellary flowers are often exserted to a length of 1 to 2 feet, so that they offer an extensive surface to wind-borne pollen. Though the stamens are separate from the carpels, they are on the same individual and the consequences of pollination between flowers on the same plant are presumably of the same order as those which follow on self-pollination. The practice of selfing in Maize is attended with considerable loss of vigour and degeneration, and as in the case of the cross-fertile clovers cited above, certain recessive factors which are responsible for dwarfness and chlorophyll deficiency soon become manifest. The method of maintaining vigour in a selected strain of Maize is to interplant it with another tested strain which is employed as the pollinating parent. Before flowering, the staminate inflorescences are removed from the selected strain. That the pollen-bearing plant will also fertilize its own carpellary flowers is immaterial, the object being to secure that its pollen will also be wind borne to the strain from which the stamens have been removed. Moreover, the selfing of the pollen parent provides a continuance of seed for pollinating the selected variety, the vigour of which is thus maintained as long as the above precautions are observed.

Another difficulty experienced in hybridization is pollen incompatibility. Here pollen grains, though functional, produce pollen tubes in the usual way, but for some reason or another, which appears to be imperfectly understood, their growth in the style is arrested, so that they fail to reach and fertilize the ovules. It has been suggested that failure may be due to the effect of a certain factor which is probably of a physiological nature. If this factor is present in the stylar tissue in which the tubes are attempting to grow, as well as in the male nuclei carried by the tubes themselves, mutual repulsion is set up, which has the effect of stopping the growth of the tubes.

Incompatibility in relation to orchard fruits has been extensively studied by Crane and Lawrence at the John Innes Horticultural Institution. These authors find that all varieties of the Sweet Cherry tested by them have proved to be self-incompatible and that the majority of our established varieties belong to groups within which all self- and cross-pollinations fail. They find also that varying degrees of incompatibility occur among apples. They point out that where fruit trees are consistently found to fail, there is a strong suspicion of inadequate pollination, and where this is suspected trees of known compatible varieties should be introduced. Hence it is better to have a mixed orchard of several varieties of apples, plums, &c., so that bees working from one variety to another may visit the blossoms indiscriminately, whereas if the varieties are more or less isolated the insects will probably confine their visits to the same variety.

The plant breeder is often limited in the range of plants capable of hybridizing. While intercrossing between strains or varieties of the same species is attended with a high degree of fertility, the same cannot be said of crossing between species and species, and between species of different genera the possibilities are still less. Even between species of the same genus, however, there may exist all grades of sterility or fertility. Outside intervarietal breeding nature appears to set up a barrier, but we have seen that this difficulty can often be surmounted by the incidence of polyploidy, when fertilization is rendered possible by somatic doubling or the fusion of unreduced gametes. Polyploidy is therefore a means by which the crossing of dissimilar types and the continuance of the hybrid combination may be accomplished. Even a chance fertile seed among many failures in a hybrid progeny may open up wide possibilities; indeed the history of some of our economic plants tells that they have emanated from fortuitous polyploid seeds.

Of extreme interest is the work of Crane and Lawrence on hybridization in the genus *Rubus*. These authors succeeded in crossing a species of diploid blackberry ($2n = 14$), namely, *Rubus rusticanus inermis*, with a tetraploid ($2n = 28$), namely, *Rubus thyrsiger*. The F_1 generation gave four hybrid seedlings of which three were *triploid* (with chromosome complement of 7 *rusticanus* plus 14 *thyrsiger* = 21) and highly sterile but not entirely so; the fourth seedling was a *tetraploid* due to an unreduced ovum (i.e. 14 chromosomes) of *rusticanus* being fertilized by haploid pollen (i.e. 14 chromosomes) of *thyrsiger*, so that with equality in the respective chromosome numbers a highly fertile and very productive form was obtained.

The phenomenon of sterility of the stamens while the carpels of the same flower may be completely fertile, or *vice versa*, is not infrequently a source of great hindrance to the hybridizer. Its presence in such plants as the potato, where the stamens are often sterile, makes genetical work on this plant very difficult, but fortunately not all varieties are barren of pollen. Crane and Lawrence report the wide occurrence of this phenomenon in several members of the *Rosaceæ*, e.g. in the Raspberry, where the presence or absence of certain genes actually determines the sex; thus normal flowers may be bisexual, but others are male, female or neuter, by suppression of the appropriate sporophylls. These authors add, however, that the female flowers fruit freely when they are grown near and are pollinated from the bisexual or the male flowers. This again emphasizes the importance of interplanting of several varieties to ensure fertilization.

We are also indebted to these authors for the light they throw on the results of the crossing of forms possessing unequal chromosome complements; triploid forms of Plum, Sloe, Damson, &c., raised from crosses between diploid and tetraploid species, and pentaploids from crosses between tetraploid and hexaploid species, have proved highly sterile, and the really productive forms have always a balanced chromosome complement. They also point out that some of our most valuable apples are of triploid constitution and sterile to a high degree, but they also indicate that in the case of pomiferous fruits, seed fertility is not so closely related to fruit production. Although in the large majority of varieties of apples and pears pollination and fertilization are necessary for fruit formation, a subsequent breakdown in embryonic growth does not always interfere with fruit formation.

We cannot within this brief review indicate even approximately the amount of progress that has already been made in plant improvement through hybridization; the reader is referred to the fascinating story of the improvement of our garden plants as told by Crane and Lawrence and to the wonderful results that have been collected by Hunter and Leake in relation to the advances made with agricultural and other plants of economic importance (see Bibliography, p. 256).

While it must be recognized that great advances have been made by selection and cultivation, the keynote of improvement is hybridization and the building up of new types. In the practice of plant breeding generally it is becoming more and more apparent that wide crosses, as between species and species, are as desirable as those between varieties, if the fullest possibilities are to be explored. To this end stress is laid on the importance of polyploidy, the intercrossing of polyploid forms, and gene mutation.

With the knowledge gained from the application of Mendelian principles and chromosome behaviour, hybridization can now be carried out on definite and profitable lines. When more becomes known of the ways and means by which polyploidy and gene mutation can be artificially induced, and when other genetic factors such as those which appear to control sterility in wide inter-specific and intergeneric crosses are elucidated, further progress in building up new and useful plants may be expected.

CHAPTER XIV

Classification of Angiosperms: Use of a Flora

Forty-three species of Flowering Plants have been selected for illustration and description in Part II of this book; they are fairly representative of the various types of floral structure in the Angiosperms. Each appears under a double name, e.g. *Viola odorata*, L., the letter L. standing for the name of the Swedish botanist, Linnaeus (1707-1778), who first gave this plant and a host of others its Latin names. Linnaeus may be said to have laid the foundations of the binomial system of naming plants, in which the two Latinized names stand for the *Genus* and *Species* respectively.

From what has already been said from an evolutionary point of view about the instability of species, and about the existence of varieties within a species, and further, of strains or races within a variety, it is obviously very difficult to say exactly what we understand by the term species.

The nearest approach to stability of type is obtained when a species becomes resolved into a number of " pure lines ", and this is probably as far as we can get towards a unit type which possesses a high degree of individuality. A pure line has at least the merits of being endowed with a uniform inheritance; but again it is extremely doubtful whether a pure or homozygous form can ever persist under natural conditions. A type homozygous in all its factors is an ideal which probably can never be attained in practice, far less under natural conditions where self-pollination is the exception and cross-pollination the rule. A pure line at best is only a mean about which fluctuations may find expression in very slight divergences.

Some method by which organisms, plant and animal, can be arranged into groups—especially if the system can be built on a basis of natural affinities—is indispensable for a study of morphology and evolution. Tentatively, a species may be said to consist of a number of near-related individuals descended from a common ancestor, sufficiently alike to be called by the same name and among which there is complete interfertility. Before genetical and cytological studies had been brought to bear upon the problems of hybridization it was usually stated that intersterility formed the strongest evidence by which true species could be separated from mere varieties. We have seen, however, that there are all degrees of fertility between types which are so different in appearance as to justify their being called different species, such types having frequently proved to be interfertile. We have only to recall the instance of the hybrid (p. 126) between the Cabbage (*Brassica oleracea*) and the Radish (*Raphanus sativus*) to realize the futility of expanding our definition of a species when we have in this example plants of a higher degree of difference, in fact individuals of different genera.

For purposes of classification the pure line may be considered as a foundation for a *sub-species* or, as it is sometimes called, a *micro-species*. The differences between sub-species are, of course, very slight and are not sufficiently striking to warrant the types being put into separate species. A number of sub-species are therefore included in the same species. The differences between one species and another are considerably wider and often take the form of well-contrasted vegetative features. Thus the species *Viola odorata*, the Sweet Violet, has long stolons; the petioles are furnished with deflexed hairs; the flowers are scented; the stigma is hooked; the spur of the corolla is straight. The species *Viola hirta*, the Hairy Violet, has no stolons; the plant is very hairy; the petioles have spreading hairs; the flowers are not scented; the spur of the corolla is hooked. These differences between the two plants are reckoned to be of specific rank and are sufficiently striking to separate these two types, but it does not follow that these particular features of contrast are applicable in all other cases. Further, all the characters of the Sweet Violet named above are common to at least four *varieties*, which, however, differ among themselves in minor details; hence the inclusion of a third *varietal* name after the specific; *Viola odorata*, var. *sulfurea*, for a variety with yellow flowers; *Viola odorata*, var. *imberbis*, for a form with no hairs on the lateral petals, and so on.

Closely related species are grouped together in a wider class or *Genus*, such as that of *Ranunculus* for all the various species of Buttercups, all of which agree very closely in the structure of their flowers. They are furnished with a calyx and corolla; there is a nectary gland at the base of each petal; the stamens are very numerous and the fruits are compound, consisting of follicles or achenes.

A comparative study of the flowers of Buttercup, Anemone, Clematis, Marsh Marigold and Monkshood (see Part II) shows that they agree very closely in fundamental structure, such as the spiral disposition of the stamens and carpels on a receptacle which is consistently cone-shaped. Further, they all possess numerous stamens and all exhibit hypogyny with free carpels. On account of this agreement in such important features of floral structure these flowers are classified in the same *Family*, which is called the *Ranunculaceæ*, after the principal or best-known genus *Ranunculus*. The above types, however, differ so widely among themselves in other features that they are placed in distinctive *Genera*. Thus the Anemone and Marsh Marigold differ from the Buttercup in that they have no corolla; again, the Anemone differs from the Marsh Marigold in the nature of its carpels and in its possession of an involucre. Such differences within a Family are deemed to be of generic rank and are wider than those which separate the various species within a genus. As a result of new discoveries relating to the morphology or the development of a given species, the systematist frequently elevates it to the rank of a genus, as for instance, the Lesser Celandine, which according to some authors (presumably on the score of its distinctive tuberous vegetative system and its possession of three sepals in place of the usual five) should be given the new generic title of *Ficaria verna*, in place of the older name of *Ranunculus Ficaria*. On the other hand, a new type, placed provisionally in a genus of its own, may on re-examination reveal features which do not warrant this isolation and point rather to its inclusion as a new species in an existing genus.

From this brief outline of the principles of classification as exemplified by the Buttercup family, it will be seen that both vegetative and floral characters are utilized. On reference to a Flora the reader will find that, in general, the process of sifting species from species follows mainly on divergences of a vegetative character, but that the allocation of species to genera and genera to families is based chiefly on similarities of floral structure. Floral characteristics afford valuable criteria for classification because they are less susceptible to change, whereas (as was described in the previous chapter) vegetative characters are more prone to fluctuate in response to varying external conditions. The more constant the features, the more valuable they are as guides for classification.

PART II

Selected Families of Angiosperms to illustrate the method of referring a Plant to its Family in using a Flora.

Class 1. **Dicotyledons.** Stem with a single ring of vascular bundles; often with secondary thickening. Leaves net-veined. Parts of the flower mostly in *fours* or *fives* or multiples of same. Embryo with a pair of cotyledons.

Division 1. APETALÆ. Corolla and often the calyx absent.

(*a*) *Flowers in Catkins*

1. *Salicaceæ.* Flowers in catkins, staminate and carpellary flowers on different plants; perianth wanting. Staminate flower consists of one or more stamens. Carpellary flower consists of two carpels united to form a unilocular ovary; ovules on two parietal placentæ. Fruit, a two-valved capsule. Trees with alternate, stipulate leaves.

(*b*) *Flowers not in Catkins*

2. *Euphorbiaceæ.* Flowers unisexual. Staminate flowers with one or more stamens. Carpellary flower with two or three united carpels; ovules one or two in each cell, pendulous. Herbs or shrubs; leaves various. Inflorescence often of many staminate and only one carpellary flower, the whole within a cup or involucre of bracts, called a *cyathium.*

Division 2. POLYPETALÆ. Flowers with, usually, both calyx and corolla present; petals free down to the base.

Sub-division 1. Flowers hypogynous; ovary superior.

(*a*) *Carpels free* (*apocarpous*)

3. *Ranunculaceæ.* Flowers regular or irregular. Stamens indefinite. Herbs with alternate leaves.

(*b*) *Carpels joined* (*syncarpous*)

4. *Cruciferæ.* Flowers regular. Sepals four. Petals four. Stamens six, four long and two short. Ovary of two carpels, bilocular; ovules in parietal placentation. Herbs with alternate, exstipulate leaves. Bracts usually wanting.

5. *Violaceæ.* Flowers irregular. Sepals, petals, and stamens, five each. Ovary of three carpels, unilocular, ovules in parietal placentation. Herbs with alternate stipulate leaves.

6. *Caryophyllaceæ.* Flowers regular. Sepals four or five. Petals four or five. Stamens eight or ten. Ovary of two to five carpels, unilocular or with imperfect septa; two to five styles; numerous ovules in central placentation. Herbs mostly with opposite leaves and stems swollen at the nodes.

Sub-division 2. Flowers perigynous or epigynous.

(*a*) *Ovary superior* (*except in some Rosaceæ*)

7. *Leguminosæ.* Flowers irregular, often papilionaceous. Stamens ten, all, or nine, of them united. Single carpel. Fruit a pod. Herbs or shrubs with alternate stipulate leaves, mostly ternate or pinnate, sometimes with tendrils.

8. *Rosaceæ.* Flowers regular. Sepals four or five. Petals four or five. Stamens indefinite, perigynous or epigynous. Ovary of one or more carpels, free or united. Fruit various. Herbs, shrubs, or trees, with alternate stipulate leaves.

(*b*) *Ovary inferior* (*epigynous*)

9. *Umbelliferæ.* Flowers regular or slightly irregular. Sepals absent, or reduced to a swollen rim, or five small points. Petals five. Stamens five. Ovary of two carpels, bilocular, inferior; styles two; one pendulous ovule in each cavity of the ovary. Fruit of two separable dry carpels. Herbs with sheathed, compound leaves. Flowers small, in umbels.

Division 3. SYMPETALÆ. Flowers with both calyx and corolla, petals more or less united into a corolla with two or more lobes.

(*a*) *Ovary superior*

10. *Primulaceæ.* Flowers regular. Calyx and corolla usually five-cleft. Stamens five, opposite the lobes of the corolla. Ovary of five carpels, unilocular, numerous ovules on a free-central placenta. Fruit a capsule. Herbs often with a rosette of leaves at the base.

11. *Solanaceæ.* Flowers regular. Calyx and corolla five-cleft. Stamens five, epipetalous. Ovary of two carpels, bilocular; ovules many, on a thick axile and oblique placenta. Fruit a capsule or a berry. Herbs with alternate leaves.

12. *Scrophulariaceæ.* Flowers irregular. Calyx four to five-lobed. Corolla four to five-lobed, often two-lipped. Stamens four, two long

and two short (rarely two or five), epipetalous. Ovary of two carpels, bilocular, style terminal; ovules numerous on a thick axile placenta. Fruit a capsule. Herbs with showy flowers.

13. *Labiatæ.* Flowers irregular. Calyx five-cleft or two-lipped. Corolla two-lipped. Stamens four, two long and two short (rarely two). Ovary of two carpels with the style between them, bilocular but later becoming four-celled, each cell with one basal ovule; stigma bifid. Fruit of four nutlets. Herbs with square stems and opposite leaves.

(*b*) *Ovary inferior*

14. *Compositæ.* Inflorescence a "head" of very small flowers (florets) surrounded by an involucre of bracts. Florets regular or irregular. Calyx absent or reduced, or represented by a pappus of silky hairs. Petals five, united, ligulate or tubular. Stamens five, epipetalous, anthers united. Ovary of two carpels, unilocular, with one basal ovule; stigma bifid. Mostly herbs.

Class II. **Monocotyledons.** Stem with scattered vascular bundles; leaves parallel-veined. Flowers with the parts in threes or fours, never in fives. Embryo with a single cotyledon.

Division 1. Flowers without a perianth, or enclosed by dry bracts or glumes.

15. *Cyperaceæ.* Perianth wanting, or represented by a number of bristles, rarely by scales. Stamens one to three. Ovary of two or three carpels, unilocular with a solitary ovule in basal placentation; single style branching into two or three papillose stigmas. Stem usually triangular and solid; leaves grass-like and sheathed, but the sheath is not split.

16. *Gramineæ.* The Grasses. Perianth probably represented by two minute scales (lodicules). Stamens usually three; anthers versatile. Ovary of a single carpel with two feathery stigmas; unilocular with a single posterior ovule. Herbs with hollow stems; leaves narrow, with sheaths split to the base.

Division 2. Perianth present, usually petaloid.

(*a*) *Ovary superior*

17. *Juncaceæ.* Perianth of six green or brown segments. Stamens usually six. Carpels three, syncarpous, ovary one to three-celled. Bushy grass-like herbs with narrow leaves.

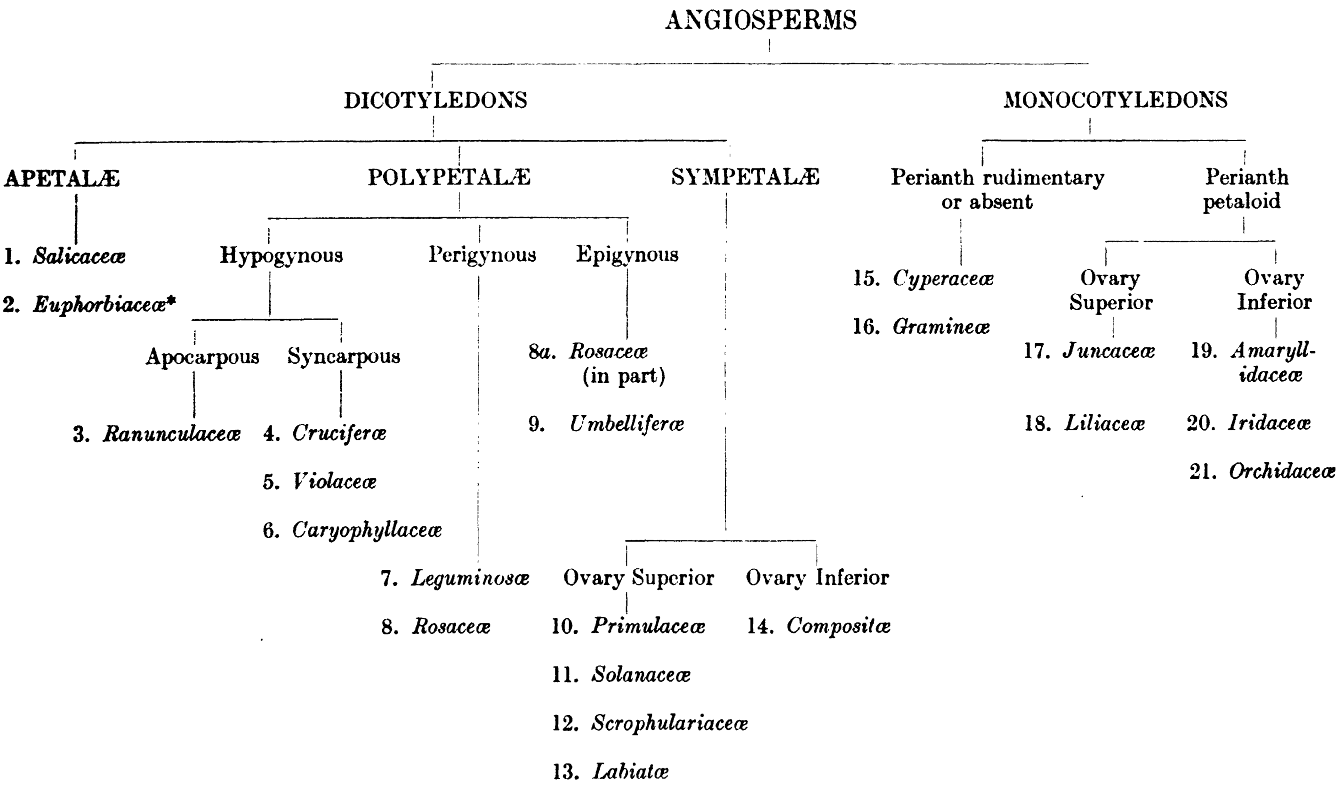
18. *Liliaceæ.* Perianth of six segments or six-cleft, petaloid. Stamens six. Carpels three, syncarpous, superior. Ovary three-celled; axile placentation. Fruit various. Herbs usually with showy flowers.

(*b*) *Ovary inferior*

19. *Amaryllidaceæ.* Perianth of six segments, petaloid. Stamens six. Carpels three, syncarpous; ovary three-celled; axile placentation. Fruit a capsule.

20. *Iridaceæ.* Perianth of six segments, petaloid. Stamens three, anthers bursting outwards. Carpels three, syncarpous; ovary three-celled; axile placentation. Fruit a capsule.

21. *Orchidaceæ.* Flowers irregular. Perianth of six segments. Stamens one (or two) adherent to the style. Ovary of three carpels, syncarpous; unilocular; ovules very numerous on three parietal placentæ. Fruit a capsule. Herbs, frequently with a tuberous rooting system.



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* This is not the correct position of the *Euphorbiaceæ*; this family is included here with the *Salicaceæ* in the *Apetalæ* merely for convenience in the use of a Flora.

DICOTYLEDONS

FAMILY 1. SALICACEÆ

The plants of this family, Willows and Poplars, are tall bushy trees, shrubs, or dwarf creeping undershrubs. The commoner types are the Goat Willow (*Salix Caprea*), growing on banks or in woods; the Osier (*Salix viminalis*), in wet places; the Bay Willow (*Salix pentandra*), in damp woods and along streams. The Poplars are tall trees of slender, pyramidal form. The Black Poplar (*Populus nigra*) and its tall variety, the Lombardy Poplar (*P. italica*), grow on the margins of streams; the White Poplar (*P. alba*), in moist woods; the Aspen (*P. tremula*), in woods and forests. The number of species and varieties of Willows is very large and several forms are natural hybrids.

Type 1. **The Bay Willow** (*Salix pentandra*, L.), fig. 36

Habit: a shrub or small tree, eight to twenty feet in height.

Inflorescence: a catkin, which is a type of spike inflorescence (fig. 5, C), in which the flowers are of very simple structure and devoid of a perianth. The staminate and carpellary catkins are on separate trees (diœcious).

(*a*) The *Staminate Catkin.* Ovoid, silky, and borne on a leafy bracteate peduncle standing erect on the branch. The catkin consists of a large number of flowers.

The *Staminate Flower* is of very simple construction, entirely devoid of a perianth, consisting of a bract covered by numerous silky hairs, a number of stamens, and a nectary. In the Willows there are usually two stamens in each flower, but in the Bay Willow there are commonly five, sometimes more; the two stamens of the Goat Willow,

Fig. 36. *Salicaceæ.*—A to H, *Salix pentandra.* A, erect staminate catkin. B staminate flower, of 5 stamens, with bract behind and a bilobed nectary gland at the base. C carpellary catkin. D carpellary flower with bract (left) and nectary (right) and forked style with bilobed papillate stigmas. E transverse section of gynœcium. F longitudinal section of ovary, showing numerous ovules in parietal placentation. G young capsule opening into two coiling valves. H ripe dehisced capsule exposing hairy seeds.
I to N, *Populus nigra.* I pendulous staminate catkin. J staminate flower of about 20 stamens inserted within a shallow cup which arises in axil of bract. K same with stamens removed from cup; *c* cup, *br* bract. L pendulous carpellary catkin. M carpellary flower consisting of a stalked cup in axil of small bract scale. N transverse section of cup ovary.

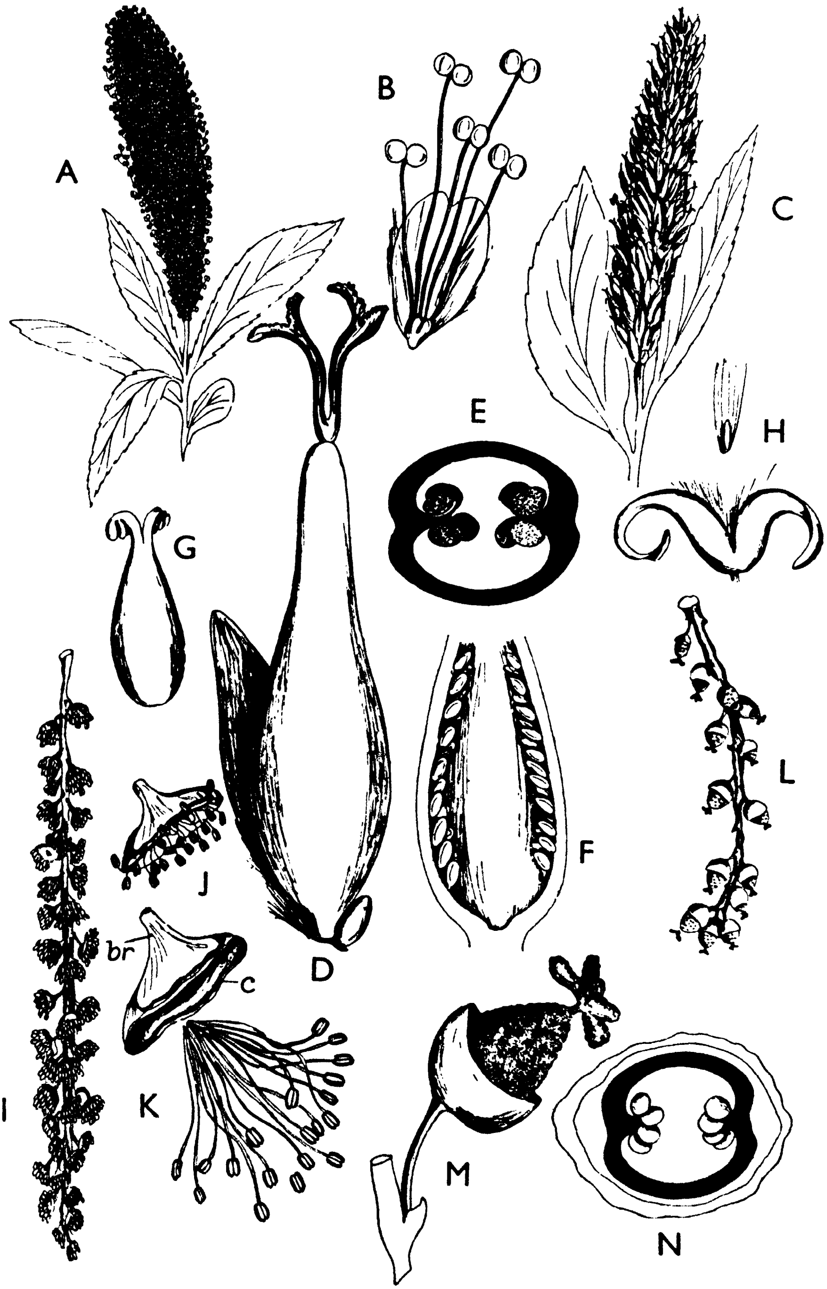

Fig. 36. (For description, see opposite)

for instance, are placed in the lateral plane of the flower. On the posterior side, that is, facing the axis of the catkin, there are, at the base of the stamens, one or two yellowish glands which exude an abundance of scented nectar through an apical pore.

(*b*) The *Carpellary Catkin* is elongated and pendulous when fully grown.

The *Carpellary Flower* also consists of a silky bract, in the axil of which is a smooth, flask-shaped, short-stalked gynœcium in which two opposite grooves indicate two joined carpels. The two horn-like styles are divergent. At the base of the superior ovary, on the posterior side, is a nectary similar to that found in the staminate flower. A transverse section of the ovary shows that it is unilocular; the numerous ovules are arranged on two parietal placentæ and from the bases of the ovules numerous hairs arise; when the fruit opens these provide a mechanism for seed dispersal.

The Bay Willow is in flower from May to June; the Osier, from April to June; the Goat Willow, from April to May.

Pollination: Willows, unlike the majority of catkin-bearing plants, are entomophilous. Bees are the dominant visitors, and various devices render the catkins conspicuous. In the majority of species the crowded anthers are of a brilliant yellow or reddish colour. In the staminate catkins of the Dwarf Willow (*Salix repens*), which inhabits sandy beaches, the crowded anthers, before dehiscence, are purple or red, at dehiscence brilliant yellow, and after the pollen is discharged, a dull inconspicuous colour. Corresponding changes may be observed in the carpellary flowers; before the stigma is mature, the wall of the ovary is of a pale-green colour; a conspicuous red colour is found when the stigma is receptive but after pollination the ovary is a dull green. The carpellary flowers are receptive for some time before the male catkins discharge pollen and thus a protogynous condition is established.

Fruit: a capsule opening by two recurved valves. The seeds are numerous and each is furnished with a tuft of hairs for wind dispersal.

Type 2. **The Black Poplar** (*Populus nigra*, L.), fig. 36

Habit: a tall tree of pyramidal form, sixty to ninety feet high.

Inflorescence: a catkin, as in the Willow; the catkins are borne on separate trees (diœcious) and appear before the leaves. Unlike those of the Willows, they are nectarless and pollination is anemophilous.

(*a*) The *Staminate Catkin* is pendulous and much longer than that of the Willow. A single flower consists of a fringed bract bearing in its axil a broad scale or disc with numerous, about twenty or more, stamens having dark-red anthers. There are no nectaries and the abundant pollen is wind-borne to the carpellary catkins.

(*b*) The *Carpellary Catkin* is also pendulous on a short stalk. The individual flowers arise in the axil of a bract. Each flower is pear-shaped and consists of two united carpels bearing two large antler-like stigmas; a cup surrounds the base of the ovary. A section across the ovary shows it to be unilocular with the ovules in parietal placentation, as in the Willow. There are no nectaries.

The Black and Lombardy Poplars are in flower in April and May; the White Poplar in March and April.

Pollination: the pendulous nature of the catkins and the broad lobes of the stigmas are well adapted for wind pollination.

Fruit: a capsule opening, as in the Willow, by two valves. The seeds are also similar, in that they bear a tuft of hairs at the base for dispersal by wind.

FAMILY 2. EUPHORBIACEÆ

The British genera, *Euphorbia* (Spurge) and *Mercurialis* (Dog's Mercury), are not very typical of the wide diversity of forms in this family. Most of them are tropical climbers or thick fleshy plants with spinous stems and leaves. Many species are poisonous and others medicinal. *Ricinus communis* yields castor oil; *Hevea brasiliensis* is the source of Para rubber; *Manihot utilissima* has roots rich in starch (arrowroot). Many forms are furnished with laticiferous tissue which stores a milky substance, latex.

Type 1. The Spurge (any species, e.g. *Euphorbia Peplus*, Petty Spurge, *E. Helioscopia*, L., Sun Spurge), fig. 37

Habit: annual herbs.

Inflorescence: a *cyathium*, bearing a marked resemblance to a bisexual flower. It consists of a cup-shaped involucre composed of five coherent pale-green bracts between four of which there are four crescent-shaped yellow glands, the nectaries. Each gland possesses two dilated, blunt horns representing the stipules of the bracts. Arising from the base of the cyathium cup is a single carpellary flower, surrounded by a number of staminate flowers with which are associated narrow, hairy scales.

(*a*) The *Staminate Flowers* arise in five groups of separate inflorescences within the cup; each group is a scorpioid cyme (fig. 5, N) of about four flowers arising in the axil of one of the five bracts; what appear to be stamens are, in fact, single staminate flowers of very simple structure, consisting merely of a stamen supported on a short stalk, the joint between filament and stalk being shown by a constriction which probably indicates the position of an aborted and now totally lost perianth; the stalk may thus be considered as a reduced receptacle of this very simple apetalous flower. Accordingly, a cyathium usually contains about twenty such flowers.

(*b*) The *Carpellary Flower* is the most conspicuous part of the cyathium inflorescence. It occupies the centre of the cup; being long-stalked it projects from the involucre and droops over the side of the cup at that point where there is no nectary between the bracts. The carpellary flower consists of the almost spherical gynœcium carried out of the cup by a curved cylindrical stalk which expands below the ovary into an indistinct ring which may represent a rudimentary perianth. The gynœcium is thus superior and consists of three united carpels; the styles, three in number, terminate in bifid stigmas. Each loculus of the trilocular ovary contains a single, pendulous, anatropous ovule with upwardly directed micropyle which is covered by a fleshy outgrowth called a caruncle, consisting partly of the integument around the micropyle and partly of the ovule-stalk (funiculus); the caruncle persists on the seed as a prominent lump.

The complete cyathium is, therefore, made up of a central cymose inflorescence consisting merely of a single carpellary flower which is surrounded by five scorpioid staminate inflorescences arising in the axils of five involucral bracts.

Pollination: entomophilous; nectar is secreted as a thin glistening film from the yellow glands. The stigmatic lobes in any one cyathium are receptive before the pollen in the same cyathium is liberated and thus the inflorescences are protogynous.

Fruit: a capsule; when ripe the three carpels separate elastically from a central column. This type of schizocarp is known as a *coccus*, for the carpels separate from the carpellary axis along with the seeds, leaving the axis behind as a central column.

Both these species are found as weeds in cultivated ground from July to October.

Fig. 37. *Euphorbiaceæ.*—A to D, *Euphorbia heterophylla.* E to G, *E. Peplus.* H to M, *Mercurialis perennis.* A, cyathium inflorescence; note that involucral cup is provided with a single stalked gland. B same in median section showing carpellary flower arising from base of cup and surrounded by staminate flowers. C group of staminate flowers forming cymose inflorescenee of about 4 flowers, with toothed scale. D staminate flower consisting of a single stamen separated from its pedicel by a constriction. E cyathium inflorescence of *E. Peplus*, showing, typically, 4 horned glands separated by bracts. F median section of a cyathium (diagrammatic) showing stalked carpellary flower; instead of the 5 staminate groups 5 inflorescence schemes are inserted to show their cymose character (actually these are as in C); the dark-shaded tips at edge of cup are the bracts. G horned gland. H staminate plant of *M. perennis*, with small clusters of flowers arising as cymes in axils of bracts. I carpellary plant with two flowers, the terminal one fruiting. J staminate bud. K staminate flower. L carpellary flower with bilocular syncarpous gynœcium. M fruit in median section with two seeds in axile placentation; note endospermous seeds with caruncles (swollen dotted part of testa).

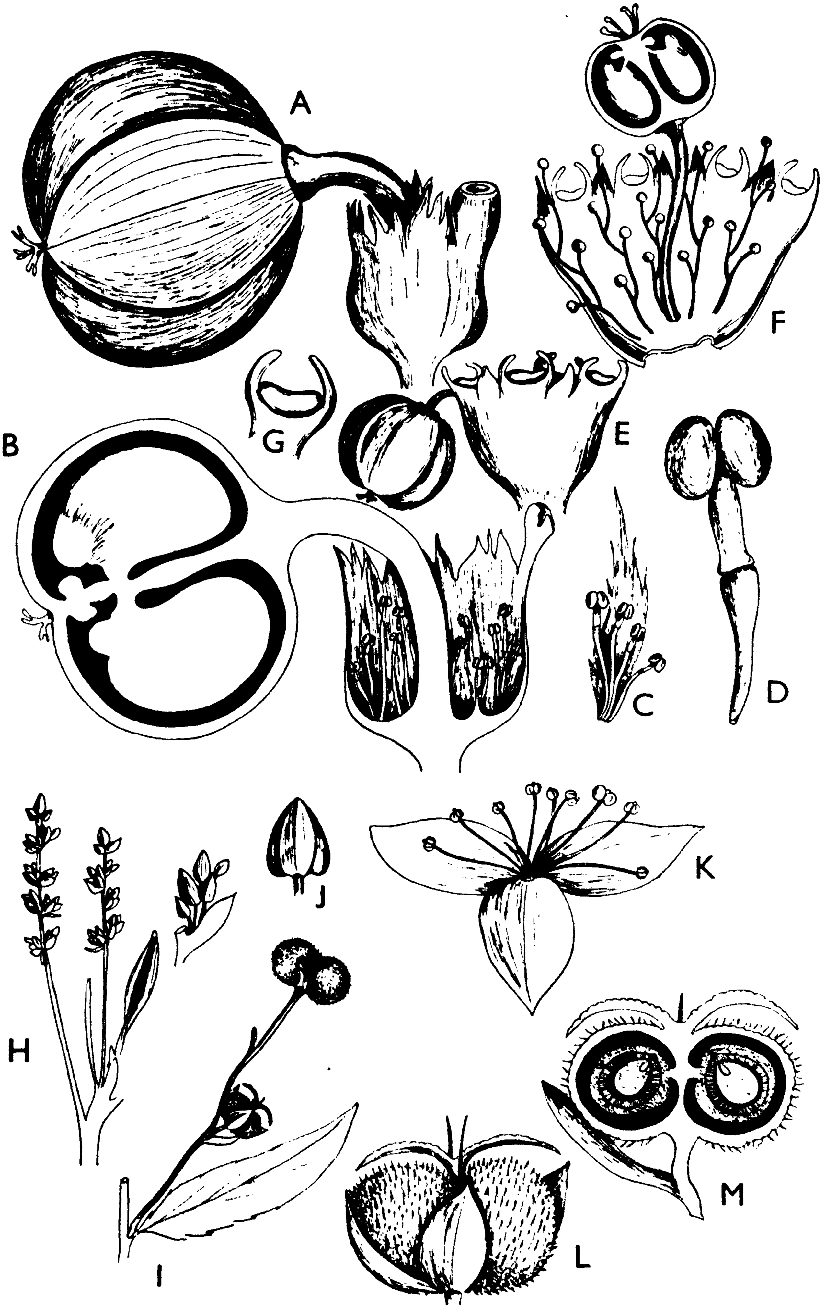

Fig. 37. (For description, see opposite)

Type 2. **The Dog's Mercury** (*Mercurialis perennis*, L.), fig. 37]

Habit: an erect perennial herb, in flower from March to May, in borders of woods.

Inflorescence: the flowers, of simple structure, occur on separate plants (diœcious). The staminate flowers are in small axillary cymes in the axils of minute bracts. The carpellary flowers arise singly and terminally, or in the axils of bracts on short branches which grow from the axils of the foliage leaves.

(*a*) The *Staminate Flower* consists of a simple perianth of three greenish segments, enclosing a variable number of stamens, a common number being nine.

(*b*) The *Carpellary Flower* arises terminally on the axis, or in the axil of a small bract. The perianth is similar to that of the staminate flower. The gynœcium consists of two united carpels bearing two divergent styles with papillate stigmatic surfaces; there are two bristles, one on each side of the ovary. The ovary wall is covered with soft hairs. A transverse section of the ovary or of the young fruit shows it to be bilocular with one ovule in each chamber. Each ovule carries a caruncle which is an outgrowth of the integument in the vicinity of the micropyle and of that part of the funiculus adjacent, the whole growth almost covering the micropyle like a lid (cf. *Euphorbia*).

Pollination: the separation of the flowers on different plants makes cross-pollination essential. The long divergent styles are well adapted to receive pollen carried by the wind.

Fruit: a capsule separating into two one-seeded portions, like that of *Euphorbia.* The seed contains a large embryo embedded in endosperm. The caruncle on the seed is rich in oil, and ants feeding on this material are instrumental in dispersal of the seeds.

FAMILY 3. RANUNCULACEÆ

Mostly perennial herbs. The flowers are built on a primitive plan, the receptacle being elongated or cone-shaped and bearing the floral members spirally, or partly spiral and partly cyclic (hemi-cyclic). The family is in advance of the *Salicaceæ* in that a perianth is developed which may further be differentiated into a distinct calyx and corolla. The flowers are hypogynous and with few exceptions actinomorphic; the stamens and carpels are numerous and arranged spirally; the carpels are free (apocarpous) and the fruits are achenes or follicles. The seeds contain endosperm.

Type 1. The Wood Anemone (*Anemone nemorosa*, L.), fig. 38

Habit: a perennial herb; in woods; flowering in April and May.

Inflorescence: solitary, on a long peduncle furnished with an involucre of three large, green leafy bracts. The flowers appear before the true leaves at the end of the rhizome.

Flower: actinomorphic; bisexual; hypogynous.

Calyx: variable, five, six, or more free sepals, pinkish-white and resembling petals (petaloid).

Corolla: absent.

Andrœcium: numerous stamens in a spiral on the elongated cone-shaped receptacle. The inner stamens at first are erect and appear to protect the carpels; the outer stamens have divergent filaments and are ripe before the inner ones.

Gynœcium: numerous green carpels, free, superior, on a continuation of the staminal spiral. Each carpel is ovoid and elongated into a conical style, and contains a single pendulous ovule together with a few small aborted ovules.

Pollination: if flowers of different ages are examined it will be found that the outermost stamens ripen first; the unripe inner stamens are erect and pressed against the carpels, which may thus be protected from receiving pollen from the outer stamens. Later, the inner stamens spread out and at this time the stigmas are exposed for cross-pollination, but it is probable that self-pollination also takes place, especially when the flowers droop. There is no honey in the flower, which is visited by bees and other insects for its pollen.

Fruit: compound, being the product of an apocarpous gynœcium. The individual carpels become dry, smooth achenes.

Type 2. The Traveller's Joy (*Clematis Vitalba*, L.), fig. 38

Habit: a woody plant climbing by means of coiling leaf-stalks; in hedges; flowering in July and August.

Inflorescence: cymose, in the axils of the foliage leaves. The main axis of the inflorescence ends in a flower, and in the axils of the two prophylls of this flower there arise one-branched monochasia.

Flower: actinomorphic; bisexual; hypogynous.

Calyx: usually four large whitish sepals, free, spirally placed on the receptacle.

Corolla: absent.

Andrœcium: numerous stamens, arranged spirally; anthers compressed.

Gynœcium: numerous carpels, free, arranged spirally; the carpels are furnished with long feathery styles; each carpel contains a single ovule.

Pollination: the flowers are visited both for pollen and for honey which is exuded in drops from the filaments of the stamens. The flowers are slightly protogynous; the outermost stamens mature first, but the inner ones appear to protect the stigmas from the pollen of the outer stamens and if bees or flies land vertically on top of the gynœcium cross-pollination may be effected, but when the inner stamens also ripen and diverge, self-pollination may also be possible, as in the Anemone.

Fruit: compound, a collection of achenes. The hairy styles are persistent and become white and feathery; the achenes are thus easily blown about by the wind.

Type 3. The Globe Flower (*Trollius europæus*, L.), fig. 39

Habit: a perennial herb; in moist woods and on banks of streams; flowering in May and June.

Inflorescence: solitary, the flowers arising singly in the axils of the foliage leaves.

Flower: actinomorphic; bisexual; hypogynous.

Calyx: five to fifteen sepals, bright yellow, free, concave in shape so that they completely enclose the other members of the flower, which is thus globular in shape.

Corolla: a variable number (about the same as of sepals) of narrow flat petals, more like stamens than petals and probably evolved from a number of the outermost stamens; they function as nectaries.

Andrœcium: numerous spirally arranged stamens.

Gynœcium: numerous spirally arranged carpels, free, each with several ovules in marginal placentation.

Pollination: the concave and strongly convergent sepals render the flower almost closed to insect visitors. In strong sunshine, however, the sepals open out a little more, and the stigmatic tips of the upwardly directed styles may be touched by pollen-laden insects which are forced to visit the flower from above. As in the previous types of this family, the inner stamens protect the stigmas, but the outermost stamens diverge and curve inwards again, so that insects probing

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Fig. 38. *Ranunculaceæ.*—A to E, *Anemone nemorosa.* A, flower of the solitary inflorescence; note tri-partite leafy bract. B median section. C stamen, front view. D dehiscence of stamen at lateral fissure. E carpel with pendulous anatropous ovule and small, aborted ovules, in unilocular ovary.

F to I, *Clematis Vitalba.* F flower, from above. G median section. H stamen with drops of nectar exuding from tissues of filament. I carpel with a single ovule in unilocular ovary; note papillate stigma and long hairs on all parts of ovary; the hairs persist on the achenes.

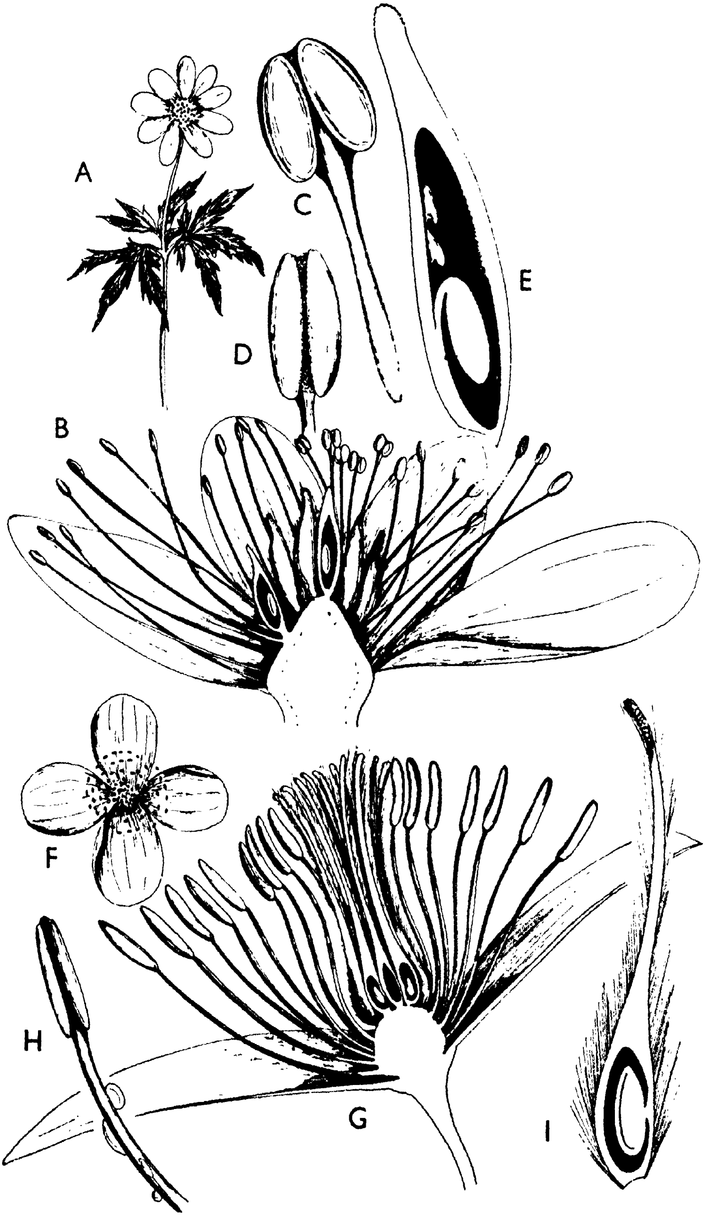

Fig. 38. (For description, see opposite)

for nectar in the petal-nectaries abutting on these stamens will at the same time collect pollen. Should cross-pollination fail the anthers of the outer stamens, in older flowers, may be thrust so far inwards as to hang over the stigmas and thus effect self-pollination.

Fruit: compound, a collection of follicles, each opening along one side, the ventral suture.

Type 4. The Marsh Marigold (*Caltha palustris*, L.), fig. 39

Habit: a perennial herb; in marshy places; flowering from March to June.

Inflorescence: cymose, in the axil of a leaf; the terminal flower is usually widely open and attended by a lateral and much younger flower, in bud.

Flower: actinomorphic; bisexual; hypogynous; all the members are arranged on a hollow cone-shaped receptacle in spiral fashion.

Calyx: the five or more yellow sepals constitute the perianth of the flower and attract insect visitors.

Corolla: absent.

Andrœcium: stamens very numerous, about one hundred, spirally arranged on the receptacle; anther dehiscence is extrorse.

Gynœcium: carpels variable in number, usually five to seven but frequently more, apocarpous, superior. Each carpel contains two rows of anatropous ovules arranged obliquely along the ventral suture. (See figs. 11, D, and 32.)

Pollination: the nectaries are present as two small groups of glandular epidermal hairs on each side of the carpel (fig. 32). The exudate is not copious and the flowers are also visited for their pollen. The outermost stamens are the first to open, shedding their pollen towards the sepals (extrorsely); at this time the stigmas are surrounded and protected by the erect and still unripe inner stamens. The outer stamens gradually curve outwards and downwards; later, the innermost stamens also curve away from the gynœcium, so that the receptive stigmas are now exposed to receive pollen carried by early bees from another flower. Self-pollination is not entirely obviated, for when the inner stamens are shedding their pollen the stigmas are still receptive, and any stamens which have failed to curve away from the carpels may deposit their pollen by contact.

Fig. 39. *Ranunculaceæ.*—A to C, *Trollius europæus.* A, flower in median section. B tubular nectary petal. C stamen; note similarity between nectary and stamen.

D to F, *Caltha palustris.* D flower in median section. E compound fruit of six follicles. F floral diagram; all the floral members are laid down along a spiral; note absence of corolla and arrangement of the numerous stamens in ranks, five deep, with extrorse dehiscence (see also fig. 14).

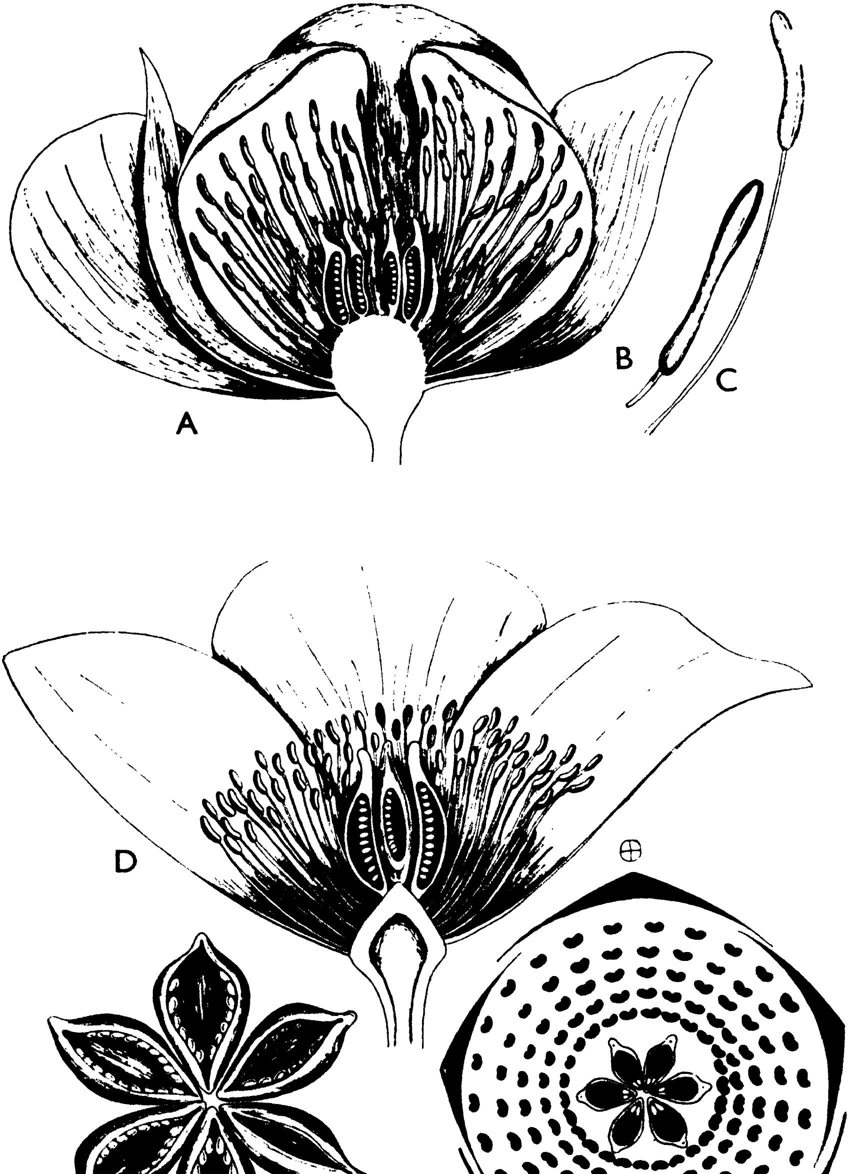

Fig. 39. (For description, see opposite)

Fruit: compound, a number of follicles which remain green and soft for a considerable time after dehiscing but which eventually become brown and dry. The follicular walls (pericarp) become crinkly and are hygroscopic, so that the numerous seeds are periodically jerked out.

Type 5. **The Monkshood** (*Aconitum Napellus*, L.), fig. 40

Habit: a perennial herb; mostly of cultivation; flowering in July and August.

Inflorescence: a raceme, together with a few axillary racemes.

Flower: strongly zygomorphic; bisexual; hypogynous; all the members are inserted on the receptacle in a spiral manner.

Calyx: five, free, deep-blue sepals; the posterior sepal is very prominent, forming a helmet or hood-like structure and overlapping at the margins the two lateral sepals, which meet together under the hood and conceal the inner members of the flower; the two anterior sepals project downwards.

Corolla: greatly modified; of about eight free petals; two, posteriorly situated, dark-blue petals are modified to form long claw-like nectaries, which, arising from the receptacle, project upwards so as to stand in close contact with the hood-sepal; each nectary-petal terminates in a horizontally projecting claw with an upwardly directed crest, and along the anterior surface of the petal is a groove leading to a nectar-supply within the dilated termination. The remaining petals are often absent or reduced to mere scales.

Andrœcium: numerous stamens with stout filaments and rather small anthers; in young flowers the stamens closely invest the carpels; pollen discharge is extrorse.

Gynœcium: three, free, superior carpels, each with numerous ovules in marginal placentation; the styles are pointed and curve outwards; the receptive surface of each style is at the extreme apex.

Pollination: the flowers are strongly zygomorphic and protandrous. The vertical orientation of the hood-sepal causes the stamens and carpels to assume a horizontal position in the flower. The outermost stamens ripen first and push out their anthers between the lateral

Fig. 40. *Ranunculaceæ. Aconitum Napellus.* A, raceme inflorescence; note also the smaller, axillary racemes. B median section, large posterior hood-shaped sepal on right; stamens protruding out of flower; note long-stalked nectary-petal sheltered by the hood. C calyx removed, exposing the two clawed nectaries on right and three of the remaining greatly reduced petals (unshaded); note that in a young flower, as here, the stamens closely surround the immature carpels.

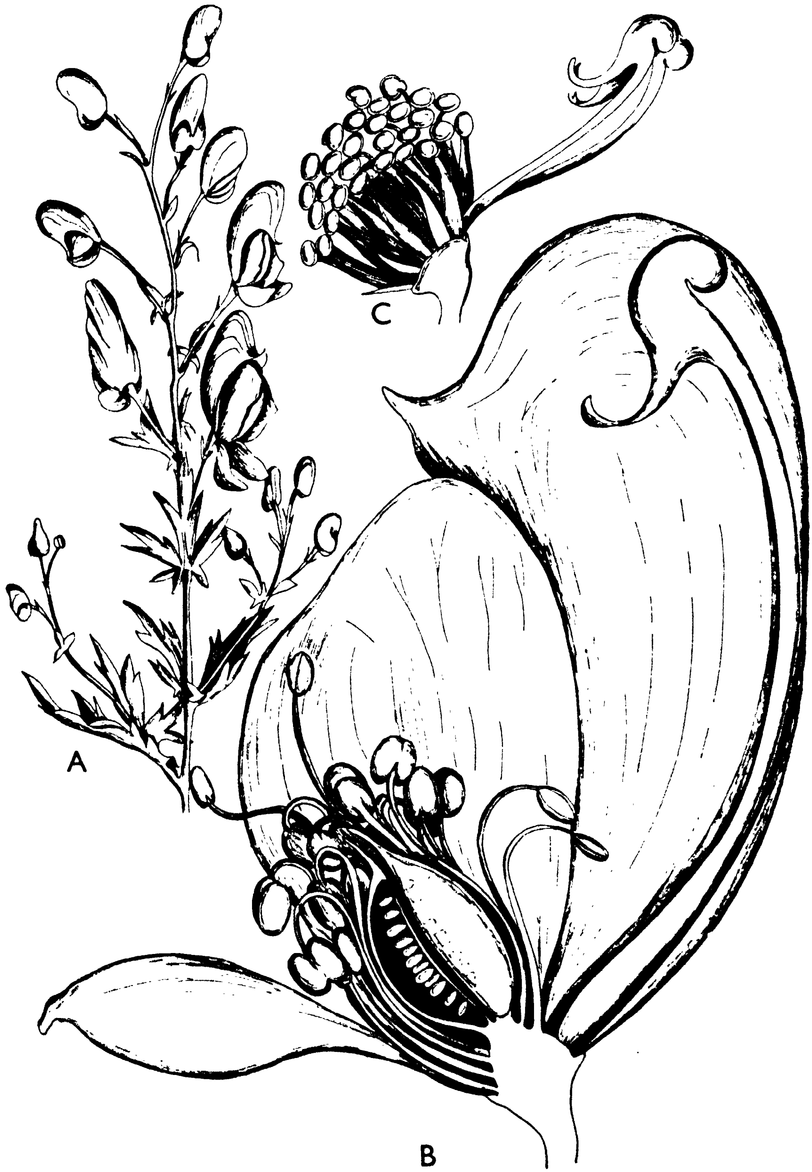

Fig. 40. (For description, see opposite)

sepals. Pollination is effected by humble bees which, alighting on the flower, grasp the two lateral sepals and thus receive pollen from the projecting anthers, on the underside of the body; the bee extracts the nectar by passing its proboscis along the groove in the nectary-stalk to the supply at the clawed end of the petal; in older flowers the now ripe, innermost stamens are also bent backwards away from the carpels, and it is only after they have shed their pollen that the stigmatic tips of the styles are receptive; cross-pollination would thus appear to be obligatory, but if some of the innermost stamens lag behind in curving away from the carpels it is possible that they may come in contact with the stigmas. A bee visiting a flower at the first stage of staminal maturity comes into touch with the anthers of the outermost ripe stamens, but at this time the stigmas are not receptive and, moreover, are protected by the surrounding inner and, as yet, immature stamens, so that self-pollination at this time is impossible. At the second stage, when all the stamens of an individual flower are withered and the carpels are exposed, the receptive stigmas are right in the path of the pollen-laden visitor, which thus effects cross-pollination.

Fruit: a number of follicles. (Cf. *Caltha.*)

Type 6. **The Lesser Celandine** (*Ranunculus Ficaria*, L.), fig. 1

Habit: a perennial herb with tuberous roots; in pastures and in waste and damp places; flowering in April and May.

Inflorescence: solitary; a single flower terminates the main shoot, and each lateral shoot also ends in a flower.

Flower: actinomorphic; bisexual; hypogynous.

Calyx: three greenish sepals, wrinkled and bulged at the base.

Corolla: about eight or nine free, yellow, glossy petals; at the base of each is a small scale, between which and the petal nectar is secreted.

Andrœcium: numerous stamens, spirally arranged; inner stamens erect and protecting the carpels; outer stamens curved outwards; dehiscence of the anthers is extrorse.

Gynœcium: numerous carpels, free, green, spirally arranged; each carpel consists of a smooth ovary, containing a single ovule; the short, blunt style terminates in a papillate stigma; the ventral groove of the carpel is continued into the stigmatic apex.

Pollination: the flowers seldom form fruits, but they are sometimes found in sunny areas. (The plant spreads profusely by means of adventitious buds found in association with the tuberous root system.) The flowers are slightly protandrous and the mechanism of pollination is similar to that of *Caltha.*

Fruit: compound; a collection of achenes; each achene encloses a single seed, which is protected by the dry wall of the fruit (pericarp). (For the illustrations of this type, see fig. 1.)

FAMILY 4. CRUCIFERÆ

Mostly herbaceous annuals, biennials, or perennials; floral structure is very uniform and characteristic; the fruit is a siliqua or a silicula; the seeds have no endosperm; the embryo is variously folded in the seed and affords a means of distinction between the genera. Shepherd's Purse, Charlock, and Mustard are common annual weeds of cultivated ground; certain biennial forms under cultivation produce greatly swollen tap roots, as in the Turnip and Swede; the Cabbage under cultivation has assumed various forms, the ordinary type having a compact bud of succulent leaves; the Brussels Sprout produces a large number of dense axillary buds on a projecting axis, and the Cauliflower forms a greatly condensed and massive inflorescence. Other genera include the Water-cress, Radish, Stock, Cuckoo-flower, Arabis, and Candytuft. The Wallflower, which offers a typical illustration of the floral structure of this family, is a perennial.

Type. The Wallflower (*Cheiranthus Cheiri*, L.), fig. 41

Habit: a perennial herb; wild on walls or old buildings; commonly cultivated; flowering in April and May.

Inflorescence: a simple raceme or corymb without bracts.

Flower: actinomorphic; the petals are placed crosswise (cruciform); bisexual; hypogynous.

Calyx: two pairs of free sepals in distinct whorls. The sepals of the outer whorl are in the antero-posterior plane; those of the inner whorl are differently shaped, being bulged or saccate at the base, and occupy the lateral plane.

Corolla: four petals, in one whorl diagonally placed in relation to the axis, and alternating with the sepals; each petal is bent at right angles into a wing or blade, and a stalk or claw.

Andrœcium: six stamens, in two whorls; two short stamens form the outer whorl, while the two pairs of taller stamens forming the inner whorl stand on each side of the median plane and alternate with the outer stamens. There are usually two nectaries, situated at the base of the two short stamens, where they form dark-green ridges, partly, or sometimes wholly, encircling the staminal filaments. Nectar is poured into the cupped, saccate bases of the two lateral sepals. The anthers open introrsely, but those of the inner stamens later curve outwards so that the anther lobes lie almost horizontally, exposing the pollen upwards.

Gynœcium: two, syncarpous, the carpels standing with their dorsal sutures laterally and therefore fused along the antero-posterior plane of the flower. The short style terminates in two papillate stigmatic lobes. A transverse section of the ovary shows that the numerous campylotropous ovules are attached to the ventral sutures in parietal placentation; the ovary, however, is bilocular owing to the formation of a thin partition which is an outgrowth from the two placental ridges *after* the ovules have appeared (*false septum*; see fig. 18). The gynœcium should be examined in median longitudinal section parallel to the plane of the septum, when the parietal ovules will be seen in two rows, and also in the lateral plane at right angles to this, when the two loculi are now seen to be separated by the septum, with the ovules recessed on the carpellary wall.

Pollination: the position of the anthers of the four taller stamens which open introrsely renders self-pollination almost inevitable, as they are on a level with the stigmatic lobes. Self-pollination is widespread in the *Cruciferæ*. Insect visitation also takes place, and it is possible that in probing for nectar at the base of the short stamens, the insect may collect pollen from the tips of their anthers; the horizontal position of the inner anthers in curling away from the style may prevent the deposit of self-pollen. The insect first touches the anthers with one side of its body and the stigma with the other and may thus bring about cross-pollination.

Fruit: a special type of bi-carpellary fruit called a siliqua. It opens from the base upwards into two valves, exposing the seeds on the parietal placentæ, now a wiry framework called the replum, across which is stretched the thin papery false septum. The seeds are without endosperm and the cotyledons are folded alongside the radicle. The flattened seeds are easily dispersed by wind. (Compare the fruit of the Shepherd's Purse, frontispiece, and fig. 34, showing a similar structure but differing in its shape and hence called a silicula.)

Fig. 41. *Cruciferæ. Cheiranthus Cheiri.*—A, racemose inflorescence. B view of flower from above, showing cruciform corolla, 2 + 4 stamens, and bilobed stigma. C calyx, side view, showing pouched sepals. D longitudinal section cut in lateral plane, i.e. through the pouched sepals; note nectaries at the base of shorter stamens; false septum cut at right angles, showing bilocular nature of ovary. E apex of gynœcium, cut longitudinally and parallel to false septum; note bilobed papillate stigmas. F siliqua fruit. G dehiscence of siliqua from base to apex into two valves; seeds in alternate arrangement on the replum. H floral diagram; formula, $K_{2+2}C_4A_{2+4}G_{(\underline{2})}$.

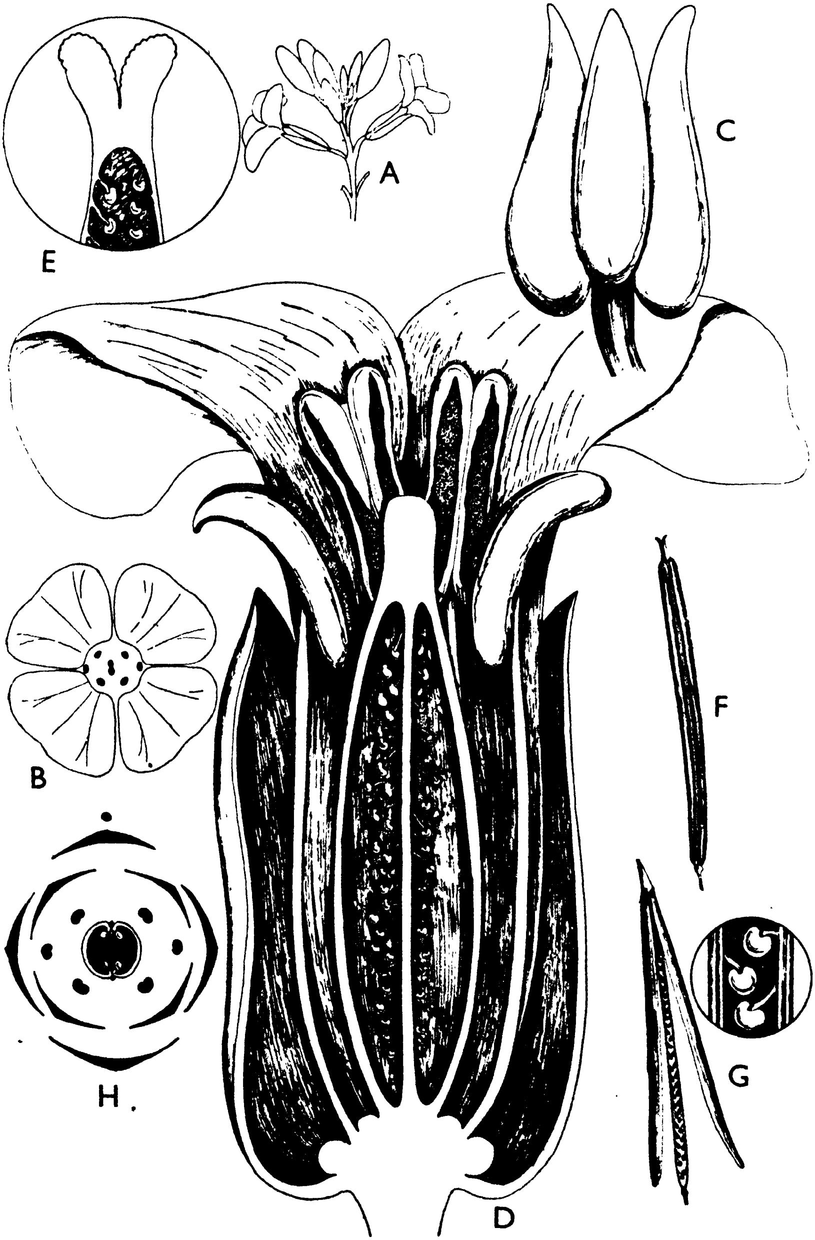

Fig. 41. (For description, see opposite)

FAMILY 5. VIOLACEÆ

A small family of annual or perennial herbs. All the British members belong to the genus *Viola*. The flowers of this genus exhibit strong zygomorphy on account of the development of a spur to the anterior petal.

Type. The Sweet Violet (*Viola odorata*, L.), fig. 42

Habit: a perennial herb with flowers of variable colour; flowering in hedges and banks from January to April. It has numerous varieties. Cleistogamous flowers are also found.

Inflorescence: solitary, the flowers arising singly in the axils of the leaves of the previous year.

Flower: zygomorphic; bisexual; hypogynous.

Calyx: five free sepals, green, furnished with appendages below their points of attachment to the receptacle.

Corolla: five free petals, alternating with the sepals; two of equal size are posterior, two are lateral and furnished with hairs which partly close the mouth of the corolla, and the fifth large anterior petal is prolonged into a spur, thus making the corolla zygomorphic.

Andrœcium: five stamens alternating with the petals; the five anthers, borne on very short stalks, converge to form a cone around the gynœcium and their connectives project upwards as triangular, brownish coloured crests which closely surround the style just below the stigmatic apex. Two of the stamens, placed anteriorly, have the basal parts of their connectives prolonged into two tails or appendages which constitute the nectaries; they pass into the spur of the anterior petal; anther dehiscence is introrse.

Gynœcium: three carpels, syncarpous; the green, ovoid ovary is concealed within the space formed by the convergent anthers; the ovary is unilocular and the anatropous ovules occur in two or more rows on three parietal placentæ; the style is hollow and terminates in a hollow dilated beak at the tip of which is the stigma; the latter

Fig. 42. *Violaceæ. Viola odorata.*—A, flower, side view; note prophylls on pedicel and sepals with downward projecting lobes. B flower from above; anterior petal prolonged into dark-shaded spur behind pedicel; in centre, entrance to spur. C centre of flower showing protruding stigmatic beak closely surrounded by anthers; two tufts of hairs on the lateral petals; note dark entrance to spur. D median section; note unilocular gynœcium with ovules in parietal placentation. E stamen showing introrse dehiscence; crest above and nectary appendage below. F bulbous stylar apex or beak showing stigmatic orifice leading into hollow style—the whole invested closely by anther crests. G three-valved capsule and seed with caruncle. H cleistogamous flower. I floral diagram; formula, $K_5C_5A_5G_{(3)}$.

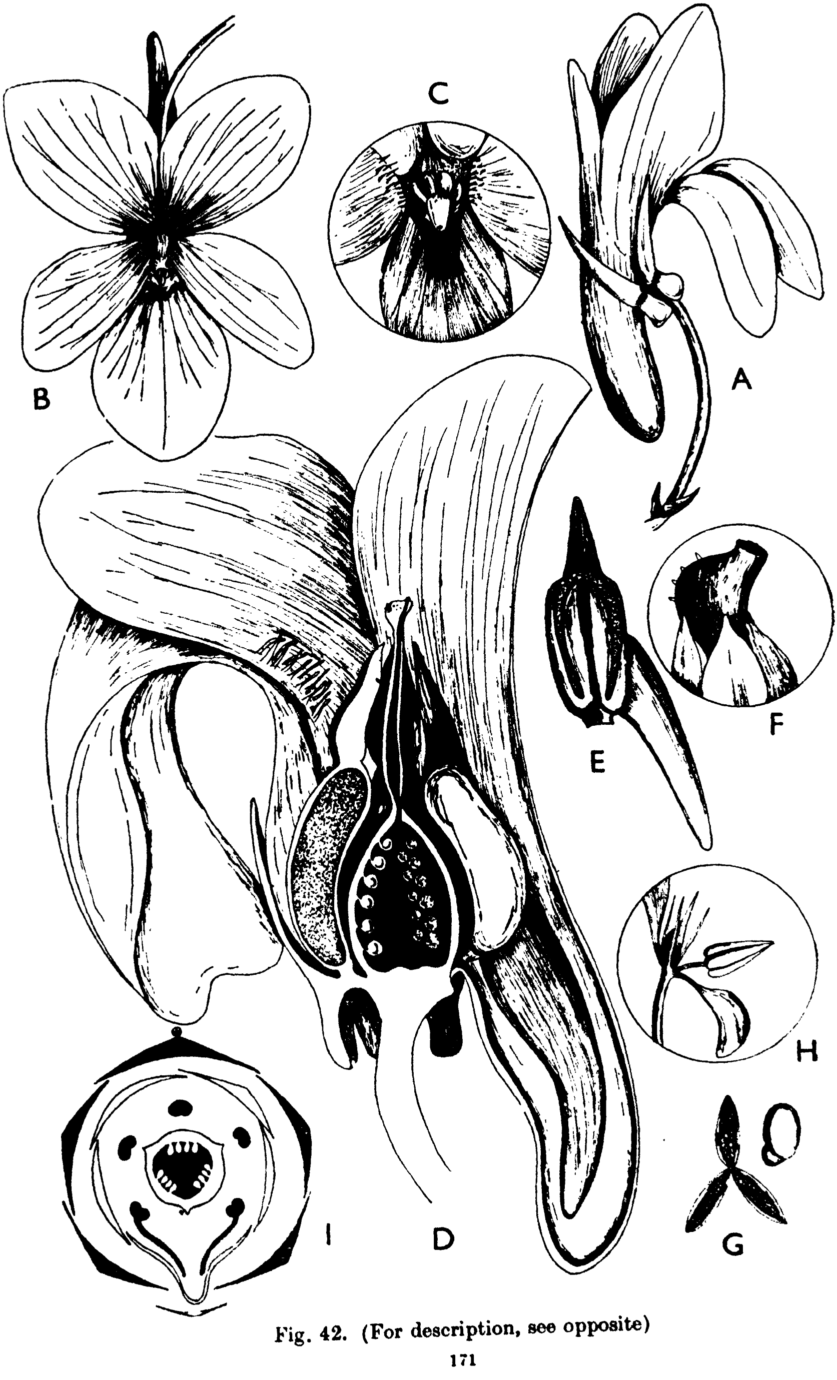

Fig. 42. (For description, see opposite)

projects above the crest-connectives and stands at the centre of the flower, fringed by the hairs on the lateral petals and just above the opening into the spurred petal.

Pollination: the flowers are scented and are visited by bees which extract nectar from the spur. The insect alights on the large spurred petal and pollen previously collected is immediately deposited on the protruding beak of the stigma; a considerable quantity of pollen is discharged introrsely by the anthers and this collects around the orifice of the spur; the bee, pushing its proboscis between the anthers, sucks nectar from the supply discharged into the spur from the staminal appendages and becomes dusted over with pollen; in withdrawing from the flower the insect may avoid contact with the receptive stigmatic beak but self-pollination is also possible, as the mechanism is not efficient to prevent contact. Moreover, the stigma is receptive at the same time as pollen-discharge, so that self-pollination must frequently take place. (In other species of *Viola* the stigmatic area is protected from self-pollen by a lid or valve which closes over the stigma when the bee makes its withdrawal.)

If cleistogamous flowers are available, note that they are much smaller than the normal flowers and are obscured by the foliage leaves. They are, of course, habitually self-pollinated but produce fertile seeds.

Fruit: a capsule opening by three valves along the dorsal sutures; each valve is thus composed of two half-carpels and bears along its median placental ridge on either side one or two rows of smooth, round seeds; the valves curl inwards at their margins and the smooth seeds are pressed out. The seeds are each furnished with a caruncle, an oil-containing body near the micropyle; the seed is endospermous.

FAMILY 6. CARYOPHYLLACEÆ

Annual or perennial herbs with swollen nodes and opposite leaves. The inflorescence is definite. There is considerable diversity in floral structure. There are two sub-families, (*a*) *Alsineæ*, with free sepals, and (*b*) *Sileneæ*, with joined sepals. In most types the two whorls of

Fig. 43. *Caryophyllaceæ. Stellaria Holostea.*—A, cymose inflorescence. B young flower bud. C flower from above. D median section; note nectary on left at base of stamen. E capsular fruit dehiscing by six teeth and protected within calyx. F seed with curved embryo embedded in perisperm. G transverse section of flower bud of *S. graminea* (axis to left); note " mesophyll " within sepals; stamens cut across their filaments; note three-lobed ovary showing broken axile septa, rendering placentation " central " and ovary unilocular. H floral diagram; note relative positions of staminal whorls; formula, $K_5C_5A_{5+5}G_{(\underline{3})}$.

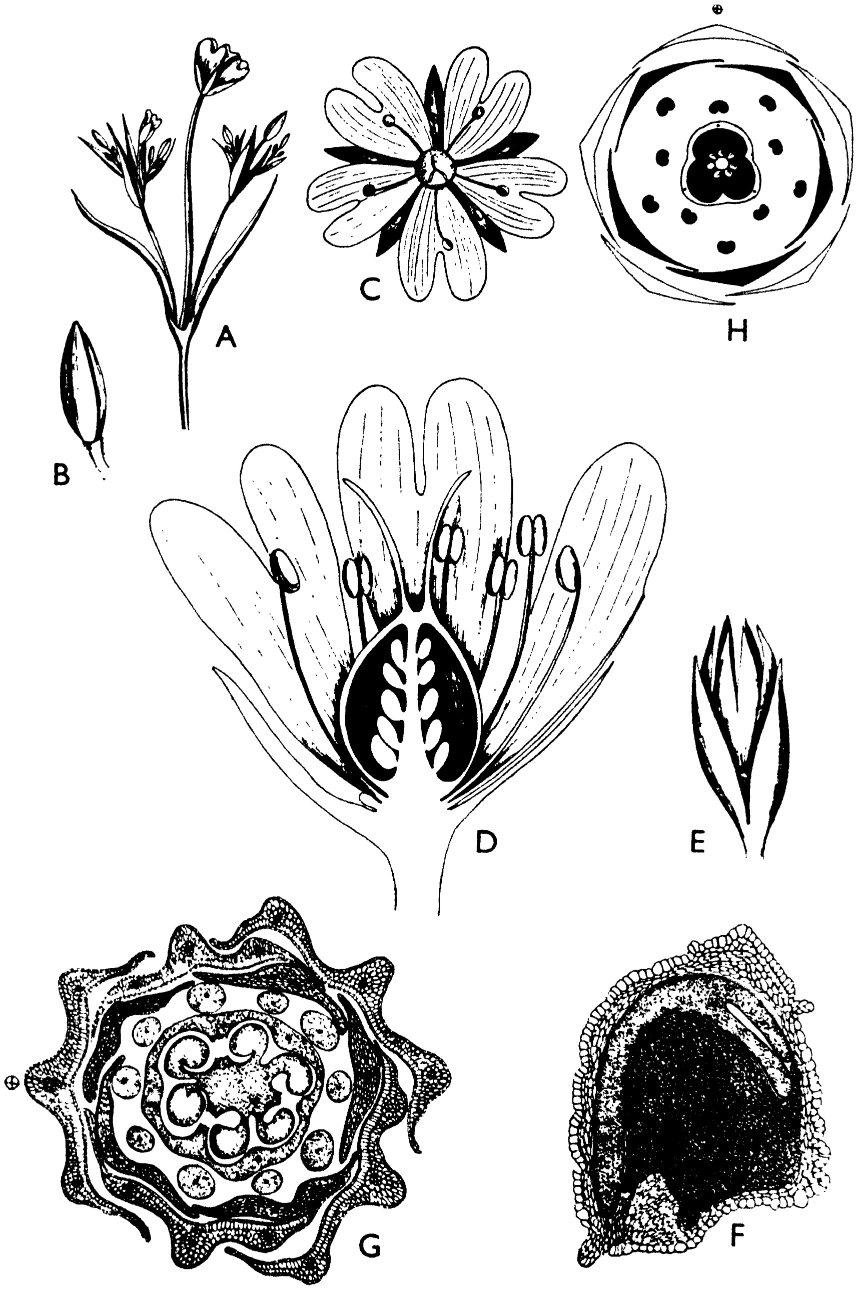

Fig. 43. (For description, see opposite)

five stamens each appear reversed in orientation; those of the outer whorl are opposite the petals and the inner whorl opposite the sepals (obdiplostemony). The gynœcium of five or fewer carpels has the ovules in central placentation, owing to the breakdown of the ovary septa; the ovules are campylotropous; the seeds contain perisperm. The family is of little economic importance.

Type 1. **The Stitchwort** (*Stellaria Holostea*, L.), fig. 43

Habit: a perennial herb flowering in hedges and in borders of woods in April and June.

Inflorescence: cymose; the main axis of the shoot terminates in a flower; from the axils of the two uppermost foliage leaves branches arise each of which ends in a flower, and these branches again bear a pair of opposite leaves, in the axils of which, in turn, flower buds arise. This regular dichasial system of branching may be further repeated with the production of still younger buds.

Flower: actinomorphic; bisexual; hypogynous.

Calyx: five green pointed sepals, free, narrowly bordered with white.

Corolla: five deeply divided, white, notched petals, alternating with the sepals.

Andrœcium: ten stamens, in two whorls of five, in regular alternation, but with apparently reversed orientation with respect to the sepals and petals (obdiplostemony); this is due to the intrusion of the inner stamens between the truly outer stamens during development; five globular nectaries are present outside the outer stamens at their bases.

Gynœcium: three carpels, syncarpous; the globular green ovary is surmounted by three divergent styles; the numerous campylotropous ovules are attached to a central placenta which has been derived from an axile type by the breakdown of the ovary septa.

Pollination: in freshly opened flowers the first anthers to dehisce are those of the five outer stamens which stand erect at the centre of the flower; in the next stage the inner stamens elongate and become erect, and when their anthers dehisce the filaments of the withered outer stamens are bent outwards. Meanwhile the stigmas are immature. When the inner stamens wither the styles elongate and diverge to expose their stigmatic tips. The flower is chiefly pollinated by flies,

Fig. 44. *Caryophyllaceæ. Lychnis Flos-cuculi.*—A, cymose inflorescence. B gamosepalous calyx. C dissected petal with two ligules. D median section; note divergent styles with papillate stigmas. E floral diagram; note gamosepaly and normal orientation of staminal whorls, and 5-lobed syncarpous ovary with central placentation. Formula, $K_{(5)}C_5A_{5+5}G_{(\underline{5})}$.

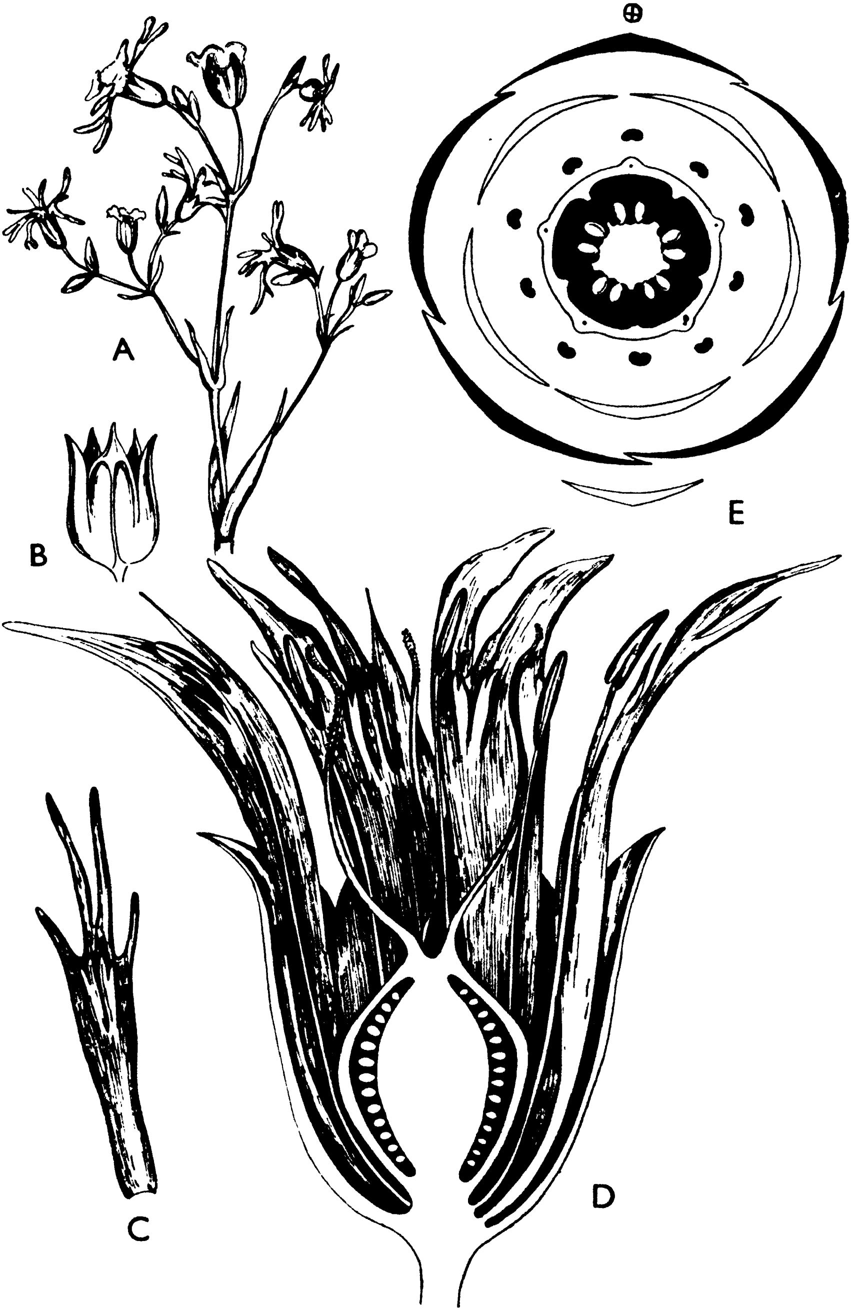

Fig. 44. (For description, see opposite)

which may carry pollen from flowers in the early stages of opening to others where the anthers are withered but in which the stigmas are receptive. Self-pollination is, however, not excluded when the inner stamens lag behind in their outward movement.

Fruit: a capsule opening into six teeth, double the number of carpels. The toothed capsule is hygroscopic; in dry air the seeds are loosened and jerked out; the teeth close over the orifice of the capsule in wet weather. The seeds are small and contain perisperm.

(*Stellaria media*, the Chickweed, a very common annual in cultivated soil, shows similar floral structure, but there is often a reduction in the number of stamens, three being quite a common number; sometimes the petals are missing.)

Type 2. **The Ragged Robin** (*Lychnis Flos-cuculi*, L.), fig. 44

Habit: a perennial herb of marshy places, flowering in May and June.

Inflorescence: cymose, built on the same plan as that of the Stitchwort, except that one of a pair of flowers at a node may be suppressed.

Flower: actinomorphic; bisexual; hypogynous.

Calyx: five sepals, joined, forming a tubular, strongly ribbed calyx protecting and supporting the weaker members of the corolla.

Corolla: five petals, red, free, with dissected or fringed lobes having a pair of scales or ligules at the junction of lobe and claw.

Andrœcium: ten stamens, in two whorls of five, in correct orientation, i.e. the outer whorl facing the sepals and the inner the petals; anther dehiscence is introrse.

Gynœcium: five carpels, syncarpous; ovary, green, broadly ovoid like an inverted cone, and furnished with five free styles which are strongly papillose on their outer surfaces for about a third of their length from the apex; the ovary is unilocular owing to the breakdown of the septa, thus rendering the placentation central.

Pollination: the flowers are protandrous and the stages in the maturing of the flowers necessary for cross-pollination are the same as for the Stitchwort.

Fruit: a toothed capsule.

Fig. 45. *Caryophyllaceæ. Silene inflata.*—A, cymose dichasial inflorescence. B flower; note inflated calyx and notched petals. C petal and its ligules. D median vertical section; note elongated receptacle and nectary at base of outer stamen. E floral diagram; formula, $K_{(5)}C_5A_{5+5}G_{(3)}$.

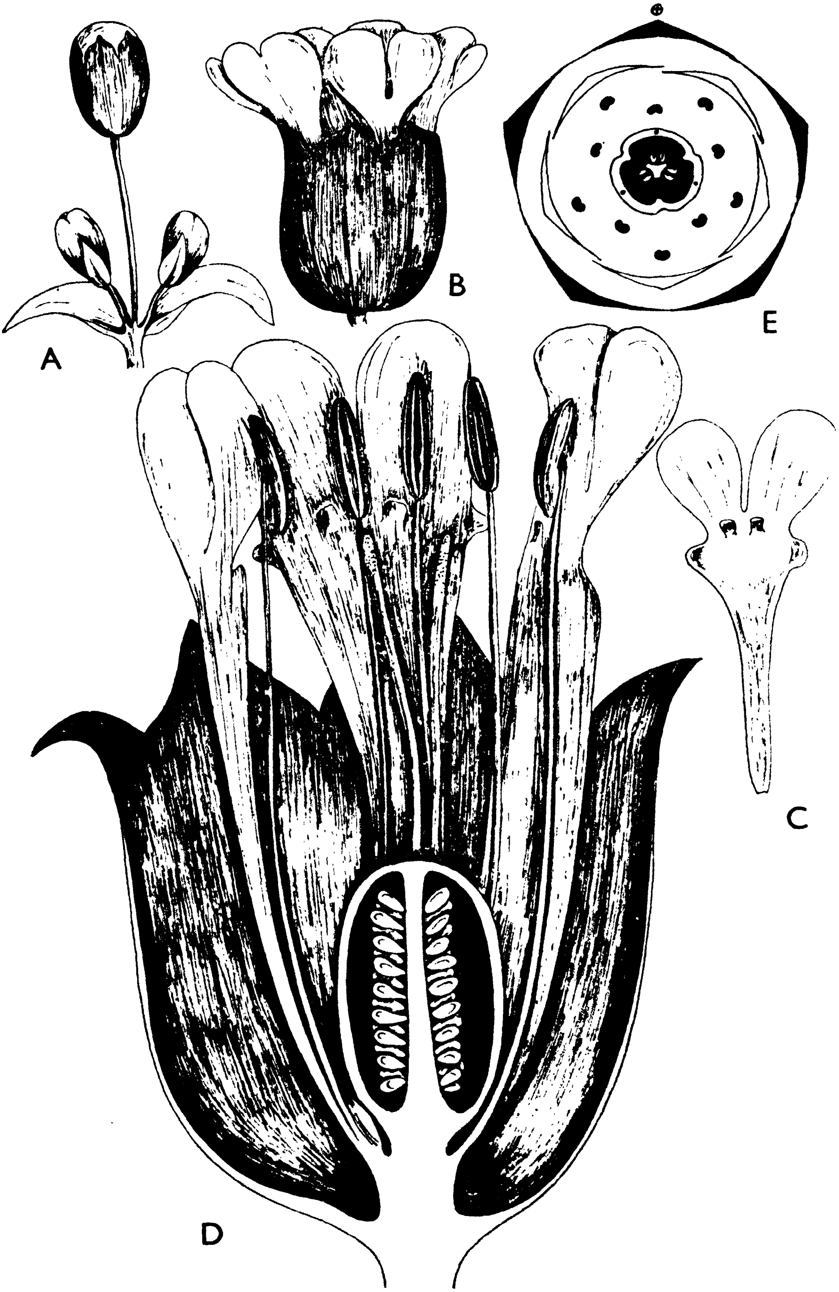

Fig. 45. (For description, see opposite)

Type 3. **The Bladder Campion** (*Silene inflata*, Sm.), fig. 45

Habit: a perennial herb; in borders of fields and waysides; in flower from June to August.

Inflorescence: cymose, a dichasium.

Flower: actinomorphic; bisexual; hypogynous.

Calyx: five light-green sepals, gamosepalous; the tubular calyx is greatly inflated and conspicuously veined, the bladder-form giving the plant its name.

Corolla: five white petals, polypetalous, each petal notched and ligulate; the petals alternate with the sepals.

Andrœcium: ten stamens in two whorls of five, the outer whorl facing the petals and the inner the sepals (obdiplostemony).

Gynœcium: three carpels, syncarpous; ovary smooth, cylindrical, and terminating in three papillose styles; the ovary is unilocular and the placentation is central, as in the previous types.

Pollination: the flowers are protandrous; the stamens ripen in two stages, first the outer five, then the inner five. Meanwhile the three styles stand erect, and as they have their receptive papillæ on the terminal portions of the styles, facing inwards, they are protected in great measure from self-pollination. When the styles diverge outwards the stamens are turned away, and if an insect after visiting a flower in the earlier stage of staminal maturity enters one at the stage of stylar divergence it comes into contact with the outspread papillose styles and cross-pollination is effected. Self-pollination, however, is not entirely obviated.

Fruit: a capsule.

Type 4. **The Red Campion** (*Lychnis dioica*, L.), fig. 46

Habit: a perennial herb; in moist woods and hedgebanks; in flower during May to August.

There are two kinds of plants, differing in height and robustness; the taller, slenderer plant usually bears only staminate flowers; the shorter, thicker-stemmed plant usually has carpellary flowers only.

Fig. 46. *Caryophyllaceæ. Lychnis dioica.*—A, *Staminate* flower in median section; floral members within calyx, raised on prolongation of receptacle; in the centre, the vestigial ovary; nectar is secreted at the hairy bases of the stamens and collects around rudimentary ovary. B *Carpellary* flower; note size relative to A; note vestiges of stamens at base of massive ovary; nectar is secreted at base of ovary. C staminate flower with calyx and corolla removed; note broad, hairy, glandular bases of filaments. D carpellary flower with calyx and corolla removed; note bluntly pointed staminodes and massive ovary with 5 erect styles. (C and D after Dr. Wardlaw.) E ten-toothed capsular fruit invested by calyx. F capsule, exposing seeds on a central placenta. Formulæ, $K_{(5)}C_5A_{5+5}G_0$ and $K_{(5)}C_5A_0G_{(5)}$.

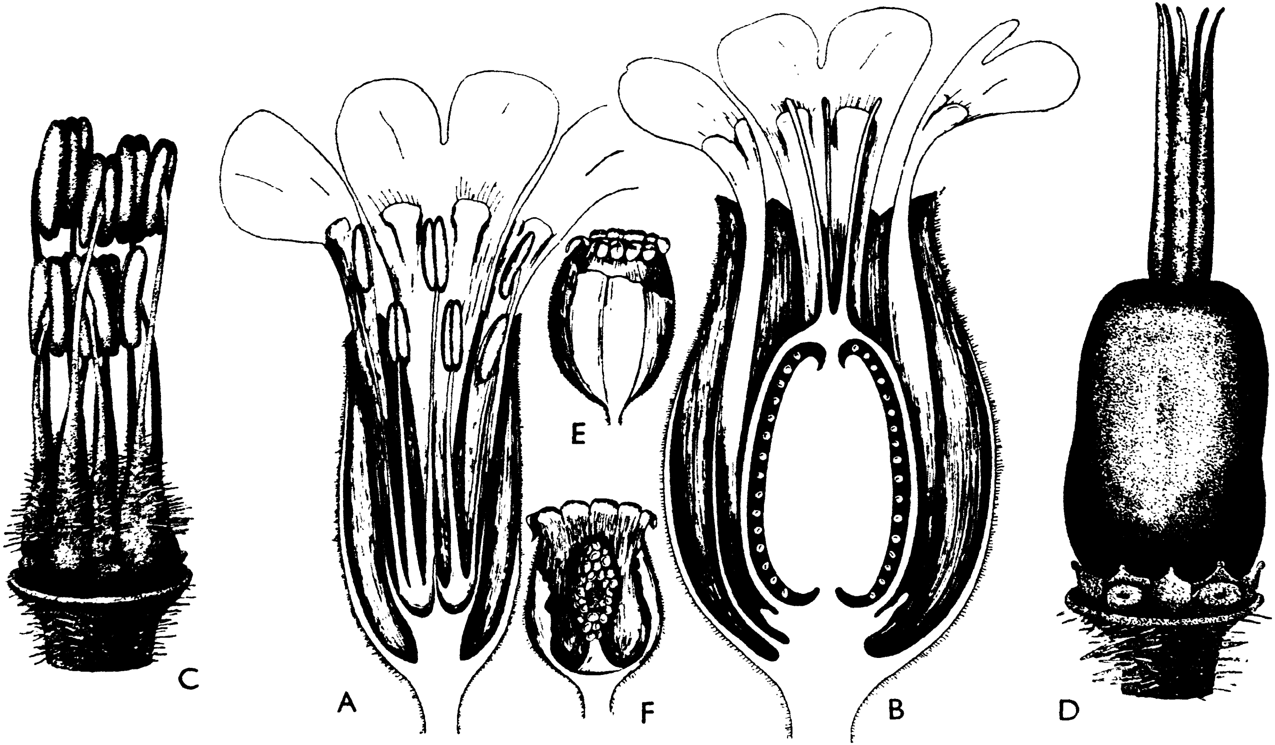

Fig. 46. (For description, see opposite)

Inflorescence: in each plant the main axis terminates in a flower, and the inflorescence is continued by axillary branches from the uppermost pair of leaves, which repeat the same type of cymose branching.

Flower: actinomorphic; unisexual; hypogynous.

Calyx: in each kind of flower there are five united sepals forming a green tubular hairy calyx.

Corolla: each flower has a polypetalous corolla of five red or rose-coloured petals furnished with ligules which partly close over the mouth of the corolla.

(*a*) The *Staminate Flower.* The corolla is raised above the level of the insertion of the calyx by an axial prolongation of the receptacle, and here too are placed the ten stamens, in two whorls of five; the stamens opposite the sepals have taller filaments than those facing the petals. At the inner bases of the stamens there are a number of nectaries joined together to form a yellow swollen rim. A small green cone standing in the centre of the flower represents a vestigial ovary.

(*b*) The *Pistillate* or *Carpellary Flower.* The internode between the calyx and corolla in the staminate flower is hardly evident here. The gynœcium consists of five united carpels and the massive green ovary is surmounted by five free styles. The ovary is unilocular and bears the campylotropous ovules in central placentation; indications of the broken axile septa may be seen towards the base of the ovary. Around the ovary near its base is a nectar-secreting rim outside which may be seen ten small white projections which probably represent the vestiges of stamens.

Pollination: the flower is visited by butterflies and hoverflies; cross-pollination is obligatory owing to the separation of the sexes on distinct plants.

Complete bisexual specimens of this species are not infrequently found.

(The dark sooty material often found in the flowers of the Red Campion (and other allied species) consists of the violet-coloured spores of the Smut fungus, *Ustilago antherarum.* The infestation is present in the anthers, the pollen being replaced by the dark-coloured spores.)

FAMILY 7. LEGUMINOSÆ

Next to the *Compositæ,* this family is the largest and most important among the Angiosperms. It contains trees, shrubs, and herbs. The British types are included in a sub-family, the *Papilionatæ,* so called from the characteristic " butterfly " shape of the " wings " of the corolla; they are largely herbaceous plants. The family is of great economic importance. The seeds are rich in starch and protein. The family includes Beans, Peas, Vetches, Ground-nut (*Arachis*), Lentil, Scarlet-runner and Clover. Many of the tropical forms (in which the family is best represented) are massive climbing plants (" lianes "); others yield useful woods, fibre, gums, resins, balsams, oils, dyes, and drugs. The roots, of the *Papilionatæ* especially, bear small tubercles which contain nitrogen-fixing bacteria. There is considerable diversity of floral structure within the family, but in the *Papilionatæ* the structure is fairly constant and characteristic.

Type 1. **The Common Broom** (*Sarothamnus scoparius*, Wimm.), fig. 47

Habit: a shrubby perennial; in heathy places; flowering in May and June.

Inflorescence: flowers solitary, in the axils of the leaves.

Flower: zygomorphic; bisexual; slightly perigynous.

Calyx: five sepals, green, gamosepalous, forming a short two-lipped tube; the posterior lip is split into two and the anterior lip into three teeth, indicating in all five sepals.

Corolla: zygomorphic, polypetalous, of five yellow petals; the general form is described as " papilionaceous ". The large posterior petal has incurved margins and folds over the other petals in the bud; it is called the " vexillum " or " standard " and is prolonged inwards into a short stalk or claw, toward which are directed a number of convergent linear markings of dark hue known as " honey-guides ", but the flower is devoid of nectar and is visited solely for pollen. The two lateral petals are known as " alæ " or " wings "; the two anterior petals are united into a " keel " or boat-shaped structure known as a " carina " which encloses the rest of the flower. Before insect visitation the petals are closely compacted and the double keel-petals close over and conceal the members of the andrœcium and gynœcium. The " wings " are interlocked with the keel on each side by a kind of " ball-and-socket " joint; the " ball " consists of a swelling at the inner margin of each wing and there is a corresponding hollow on each side of the keel to receive this (see fig. 47, C & I); the wings and the keel are thus closely articulated.

Andrœcium: ten stamens, all joined, the basal parts of the filaments united to form a staminal tube; the filaments vary in length; when the staminal tube is split open, it is seen that the stamens occur alternately, five short and five long, but one of the latter is intermediate in size and is situated exactly anteriorly. In the flower-bud all the stamens curve inwards in conformity with the shape of the "keel" petals. The staminal tube invests the ovary closely, but it is inserted on the receptacle at a slight distance away from the base of the ovary, thus making the stamens slightly perigynous.

Gynœcium: a single, unilocular carpel with a narrow, green, elongated ovary, strongly compressed laterally and curved along its posterior margin, where two rows of ovules arise in marginal placentation. The style is long and curved inwards in close contact with the keel; it ends in a narrow club-shaped portion flattened on its inner side like a small shallow spoon; the receptive stigmatic part is at the extreme tip of the spoon and is slightly papillose.

Pollination: the nectarless flower is visited for pollen by various kinds of bees. The curved tip of the style fits closely within the apex of the keel; the curved stamens, being also imprisoned within the closed carina, are in a state of tension, as is also the tip of the style, which presses hard against the keel like a coiled spring. The bee, preferably of the heavier type like the humble-bee, alights on the two wings, and on account of the articulations between wings and keel the weight of the insect causes the joined inner margins of the keel to separate; the splitting of the closed keel starts from the inner part and finishes off at the tip. This progressive opening of the keel causes first the quick release of the shorter stamens, which strike the bee and throw their pollen on to the ventral side of its body. As the keel continues to open, the long stamens and the curved style are now explosively released, and the pollen from these stamens is thrown on to the bee's back. The coiled style, however, under greater tension, escapes from the keel *a moment in advance* of the stamens, and if the visitor is already laden with pollen from another flower this pollen is picked up by the stigmatic extremity of the style before the bee receives pollen from the flower visited. As soon as the style has been liberated from the keel it may curve further and cross itself like a loop so that the stigmatic tip is now uppermost and may thus escape being self-pollinated; it is, however, doubtful if selfing can be entirely obviated, as the pollen is discharged from the anthers in a shower. The whole mechanism of pollination is explosive and is actuated by the weight of

Fig. 47. *Leguminosæ. Sarothamnus scoparius.*—A, flower bud, side view. B gamosepalous calyx, with 3 anterior and 2 posterior teeth. C zygomorphic, papilionaceous corolla, posterior "vexillum" or "standard" at the top, "alae" or wings in lateral position, and 2-petalled keel or carina placed anteriorly; note articulations between wings and keel. D andrœcium, staminal tube opened out; the anterior, medium-sized stamen in middle opposite anterior sepal; the taller stamens stand opposite the petals; the short stamens face the sepals. E staminal tube enclosing gynœcium; note curved style. F the carpel with curved style terminating in flattened stigmatic tip; ovules in marginal placentation. G median section; note slight perigyny and position of anthers of long stamens in relation to curved tip of style within tip of keel; unilocular ovary with ovules in marginal placentation. H opened legume. I floral diagram; floral formula, $K_{(5)}C_5A_{(10)}G_{\underline{1}}$.

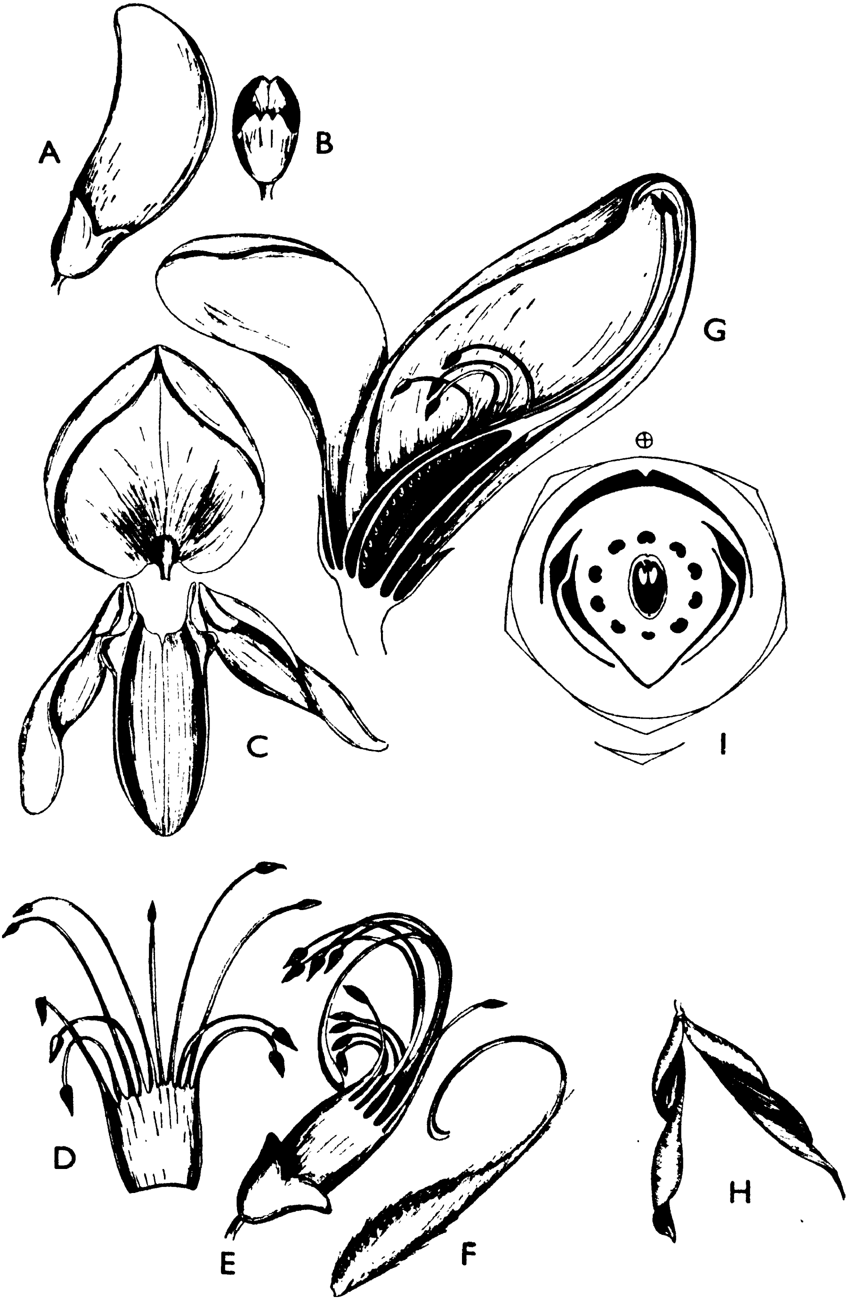

Fig. 47. (For description, see opposite)

the bee on the wings causing the closed keel to release the stamens under tension, but the operation cannot be repeated as the articulations between wings and keel cannot be restored. Pollinated flowers of the Broom can be distinguished from those unvisited because their petals are seen to hang limply; such flowers eventually bear seed. Flowers not visited seldom set fruit, so that self-pollination in general appears to be obviated and the mechanism for cross-pollination seems to be a highly effective one. Flowers in which the mechanism has not been worked do not form seed.

Fruit: a pod, or legume, opening along both dorsal and ventral sutures into two valves which soon become spirally coiled; the marked hygroscopy of the twisted valves causes the marginally attached seeds to be flung a considerable distance.

Type 2. **The Gorse** or **Whin** (*Ulex europæus*, L.), fig. 48

Habit: a perennial shrub with spinous leaves and branches, flowering for a long period, usually from February to July; on heaths.

Inflorescence: the solitary flowers arise in the axils of the leaves of the preceding year's shoot.

Flower: zygomorphic; bisexual; perigynous; two bracteoles are present on the pedicel just below the calyx.

Calyx: deeply two-lobed, yellow, covered with short brown hairs. The lobes are minutely toothed; the posterior lobe represents two, and the anterior lobe three, almost completely joined sepals.

Corolla: zygomorphic, papilionaceous, yellow in colour, and interlocking as in the Broom.

Andrœcium: ten stamens all joined at the base by a staminal tube. The stamens are alternately long and short; the anthers of the taller stamens are cylindrical and larger than those of the short stamens, which are conical.

Gynœcium: a single unilocular carpel with a short ovary thickly covered with hairs; the style is bent and ends in a globular stigma; the ovules are in marginal placentation.

Pollination: there is no honey, and the flowers are visited chiefly by hive bees for the pollen. The mechanism is of the same nature as in the Broom and is only operative once. It is, however, not nearly

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Fig. 48. *Leguminosæ. Ulex europæus.*—A, flower in side view, showing hairy calyx and one of the two prophylls below; note protruding stigma. B petals, large posterior standard, lateral wings or alæ, anterior keel or carina of two partially joined petals; note articulations in wings and keel. C staminal tube of ten stamens (5 short and 5 long) opened out. D staminal tube enclosing gynœcium. E the single carpel with knob stigma. F median section; note slight perigyny. G floral diagram, showing lateral prophylls. Floral formula, $K_{(5)}C_5A_{(10)}G_{(\underline{1})}$.

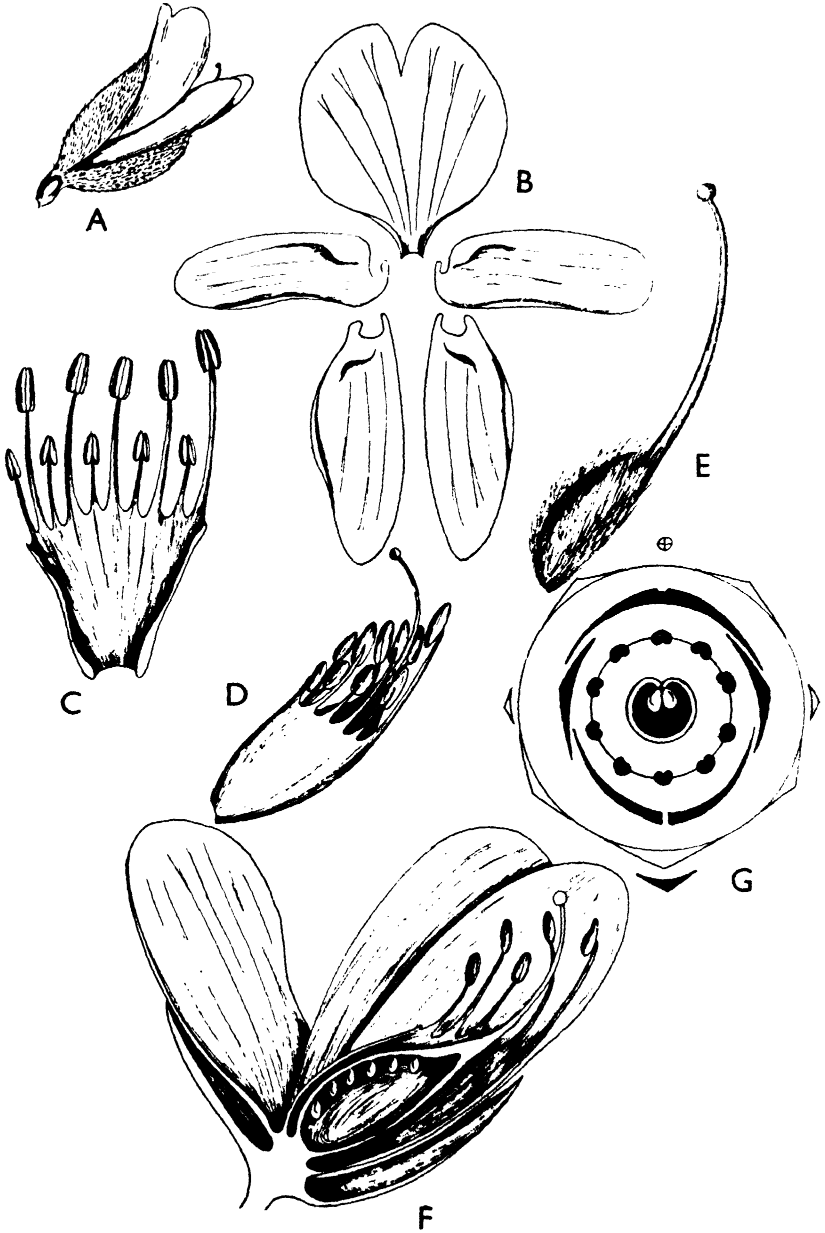


Fig. 48. (For description, see opposite)

so explosive in its action. The weight of the insect astride the wings depresses the keel and the style emerges first so that it touches the insect on the under side of the body and cross-pollination is immediately effected. The shorter stamens then emerge, followed by the longer stamens, the insect receiving pollen on the under part of the body. The next flower visited is therefore certain to pick up pollen, as the stigma is the first part to protrude.

Fruit: a legume containing a few seeds; the legumes are audibly explosive in their dehiscence.

Type 3. The Lupin (*Lupinus polyphyllus*, L.), fig. 49

Habit: a perennial shrub of cultivation, flowering in June.

Inflorescence: a dense raceme of flowers in whorls of about six, close together when young but later separated by elongation of the internodes into a massive inflorescence. Each flower arises in the axil of a bract which falls off as the flower matures; the bracts are still in evidence at the top of the inflorescence; some larger sterile bracts may be found towards the base of the axis.

Flower: zygomorphic, strongly compressed laterally so that the posterior petal is deeply grooved; bisexual; perigynous.

Calyx: deeply bilobed; green; the anterior lobe projects strongly forward but there is no indication of teeth to signify its equivalence with three sepals as in the Broom; the erect, posterior lobe is, however, distinctly notched, indicating the usual two sepals of the posterior part of the calyx.

Corolla: variously coloured; papilionaceous; petals free; the posterior petal is strongly compressed laterally and its margins are incurved; the two wings are convex outwardly, and stand close together and erect in the laterally extended flower; the carina (keel), also vertical, is almost entirely concealed by the wings. The keel and wings are articulated together as in the Broom and Gorse; the upper margins of the keel are only partially joined and towards the tip there is a small gap or aperture.

Andrœcium: ten stamens joined together by a basal staminal tube, as in the other types. The filaments vary in length; five shorter stamens reach about halfway up, and five taller ones extend nearly the whole

Fig. 49. *Leguminosæ. Lupinus polyphyllus.*—A, racemose inflorescence. B flower from above; deeply folded " standard " at top, wings embracing keel. C deeply cleft bilobed calyx. D outline of flower when the wings are depressed as by insect visitation; note protruding pollen mass (piston-mechanism). E median section; note tip of style surrounded by the longer stamens. F tip of style (knob) protected by circlet of hairs. G floral diagram. Floral formula, $K_{(2+1)}C_5A_{(10)}G_{\underline{1}}$.

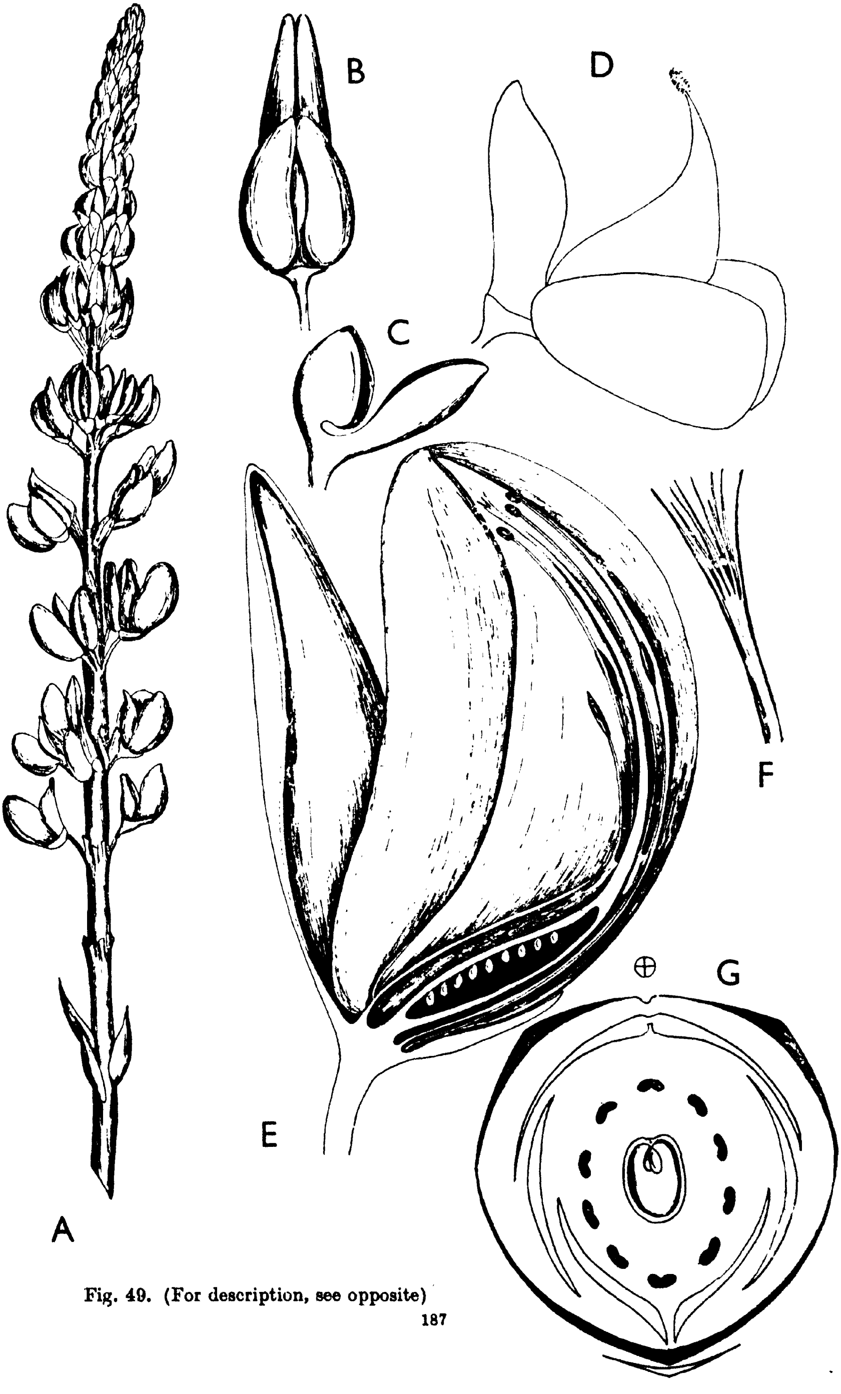


Fig. 49. (For description, see opposite)

length of, the carina which encloses them. Moreover, the anthers of the short stamens are much longer than those of the taller stamens. During the flowering period the filaments of all the stamens are capable of extension by growth. The insertion of the staminal tube on the receptacle is slightly removed from the ovary base, so that the flower is perigynous.

Gynœcium: a single carpel, unilocular, enclosed by the staminal tube. The style is firm and rigid and is curved almost at right angles to the long axis of the ovary. The style ends in a globular stigma which is strongly guarded by a circlet of closely-set, forwardly-projecting bristles. The ovules are in two rows along the ventral margin.

Pollination: the flower is visited solely for its orange-coloured pollen. Pollination is effected by a " piston-mechanism " which is operated by the heavier type of insect, the humble bee. The stamens do not all ripen at the same time; the short stamens with their large anthers discharge their copious pollen into the middle part of the keel, and then the taller stamens liberate their pollen into the end of the keel. The shorter stamens now lengthen their filaments by intercalary growth, and their extension within the keel acts as a piston, the head of which is formed of their compacted anthers, which now proceed to pack the extremity of the carina with their pollen. Although the stigmatic lobe occupies the extremity of the carina it is protected from the pollen below it by its circlet of bristles. The bee alighting on the wings depresses the keel and the first part to emerge is the stylar tip with the terminal stigma, which may thus receive pollen if the visitor has already received pollen on the ventral part of its body from another flower. The insect's weight on the wings causes the retraction of the keel over the end of the anther-piston, and the bright orange pollen in the form of a sticky cylindrical mass is pushed out through the aperture in the tip of the keel. The pollen is thus picked up by the bee on the ventral part of its body. Unlike the Broom and Gorse, the piston mechanism can be operated several times, for when the insect flies away the keel returns into its articulations with the wings, and the piston (formed of the stamens and anthers) recedes into position behind the pollen mass. When the style returns into the keel, now packed with pollen, it is, of course, subject to self-pollination, but meanwhile cross-pollination has been effected.

Fruit: a legume, dehiscing as in the Broom.

Other leguminous flowers, such as the Garden Pea, Broad Bean, Sweet Pea, &c., are constructed on the same plan as the foregoing types, except that the staminal tube is split along its posterior side and unites only nine of the ten stamens, the odd stamen being free and attached independently to the receptacle just above the split. Moreover, these flowers contain nectar, which is secreted around the base of the ovary and is collected within the staminal tube. Visiting insects probing for nectar first touch the stigma and effect cross-pollination. Self-pollination is, however, very widespread in these types and the flowers of the edible pea and bean are habitually self-pollinated.

FAMILY 8. ROSACEÆ

A large family of diverse habit containing herbs, shrubs, and trees, with simple or compound stipulate leaves. It includes a large number of our economic fruit-bearing plants, e.g. Plum, Cherry, Sloe, Raspberry, Blackberry, Strawberry, Apple and Pear. The genus *Rosa* contains a very large number of species and varieties of wild and cultivated roses. Meadow-sweet, Wood and Water Avens, Silverweed, Tormentil, Lady's Mantle are common wild herbaceous plants; the Mountain Ash, White Beam, Service Tree, Medlar, and Hawthorn are representatives of the tree types.

The shape of the floral receptacle and the position of the members in relation to the carpels accounts for the division into several sub-families. Perigyny is a conspicuous feature, but epigyny is also exhibited in the sub-family *Pomoideæ*, which includes the Apple and Pear. There is a wide range in the character of the fruit, with which the receptacle is frequently associated permanently. The stamens are usually numerous and the carpels range from one to numerous. The seeds are usually exalbuminous.

Type 1. **The Dog Rose** (*Rosa canina*, L.), fig. 50

Habit: a prickly shrub, varying considerably in foliage; in hedges; flowering in June and July.

Inflorescence: solitary, at the end of a branch or in small terminal cymes.

Flower: actinomorphic; bisexual; strongly perigynous; the receptacle is flask-shaped with a narrow orifice.

Calyx: five free green sepals, on the edge of the receptacular flask; they differ in the character of the margin, some sepals being smooth and others fringed or partly fringed; in the fully expanded flower they are reflexed.

Corolla: five free, pink or white petals, alternating with the sepals; each petal is slightly bilobed.

Andrœcium: numerous stamens, curved inwards in the bud; arranged in two or three whorls in regular cyclic arrangement, on the inner edge of the receptacle, but leaving a clear space around the orifice; this area, known as the " disc ", has a shiny surface and appears like a nectary but there is no secretion of nectar. There are usually ten stamens to each whorl; those in the outer whorl stand in pairs opposite the five petals, and the stamens in the succeeding whorls follow in alternation; the anthers are broad with introrse dehiscence.

Gynœcium: numerous free carpels concealed within the receptacle, to the base and sides of which they are attached; each carpel is shortly stalked and the unilocular ovary contains one or two ovules in pendulous placentation. The terminations of the styles pass through the orifice of the receptacle as a small brush and form the stigmas.

Pollination: the flower contains no nectar. As the bud unfolds, the inwardly curved stamens diverge, so that the brush of stigmas from the several carpels becomes fully exposed at the centre of the flower, and an insect alighting on the centre may thus effect cross-pollination. If the stamens are tardy in their outward movements self-pollination is possible when the anthers stand immediately above the stigmas. It appears, however, that the flowers may be sterile to their own pollen, cross-pollination alone being effective. Hybrid-forms are very prevalent in nature.

Fruit: compound, consisting of a number of hairy achenes each the derivative of a single carpel; they remain within the receptacle, which changes colour from green to red. Birds peck at the juicy receptacle and the achenes may be disseminated in this way.

Type 2. **The Blackberry** or **Bramble** (*Rubus fruticosus*, L.), fig. 50

Habit: a scrambling shrub furnished with stiff prickles; in hedges and woods; flowering from July to September; numerous varieties exist.

Inflorescence: a number of axillary cymes of two or three flowers, arising in the axils of reduced leaves at the ends of the branches.

Flower: actinomorphic; bisexual; strongly perigynous; the broadly concave receptacle bears a central cylindrical portion on which the numerous carpels are situated.

Calyx: five, free, at the outer rim of the expanded receptacle, reflexed when the flower is fully open.

Fig. 50. *Rosaceæ.* A to F. *Rosa canina.*—A, flower with urn-shaped receptacle. B same from above; disc, surrounded by sepals. C median section. D single carpel. E pseudocarp enclosing achenes. F achene; basal part of fruit. Floral formula, $K_5C_5A_\infty G_\infty$.

G to I. *Rubus fruticosus.*—G median section of flower. H single carpel with expanded stigma at apex. I portion of compound fruit composed of drupels: at right, one drupel, seed embedded in stony endocarp, soft mesocarp, and outer epicarp. Floral formula as for Rose.

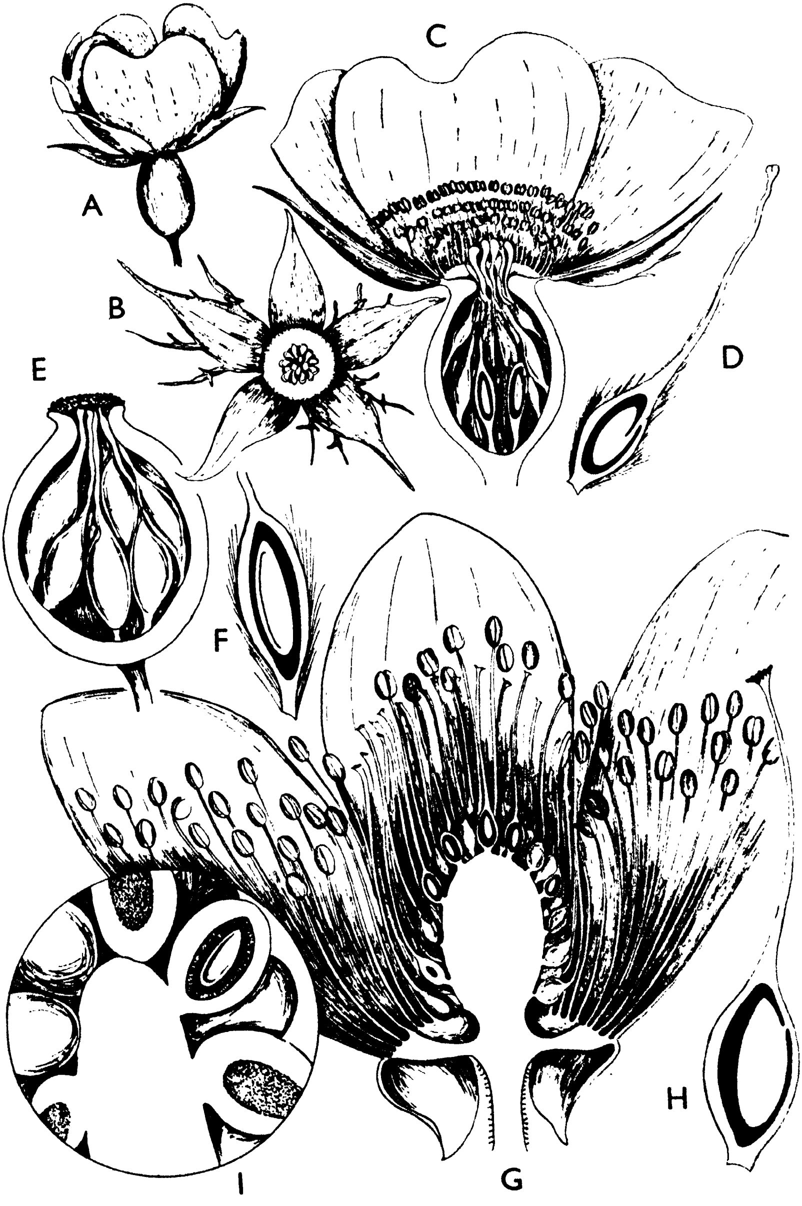


Fig. 50. (For description, see opposite)

Corolla: five, pink or white, polypetalous, alternating with the sepals.

Andrœcium: numerous, in several whorls on the margin of the concave part of the receptacle; the stamens are often branched; dehiscence of the anthers is introrse.

Gynœcium: numerous small ovoid carpels, apocarpous, each carpel containing two ovules in pendulous placentation. The styles are hairy and terminate in expanded stigmas. The carpels are confined to the central, cylindrical part of the receptacle and are superior. The relative position of the other floral members, which are distantly placed from the carpels, makes the flower strongly perigynous.

Pollination: the flowers are greatly frequented by numerous small and long-tongued insects. Nectar is secreted on the inner surface of the concave part of the receptacle. The stamens of the outer whorls have longer filaments than the rest; they diverge widely when the flowers open, and they are the first to shed pollen. At this time the styles are erect and closely compacted, so that cross-pollination is possible if the visiting insect alights directly on the exposed brush of stigmas, for the surrounding inner stamens are still immature. Self-pollination is, however, possible when the inner stamens ripen, especially if they lag behind in their movement away from the carpels.

Spontaneous hybridization is prevalent in this genus and there are several varieties.

Fruit: compound (being the product of an apocarpous gynœcium); a collection of small succulent drupes or drupels. They are attached to the receptacle which still bears the reflexed calyx. The drupels are disseminated by birds.

Type 3. **The Water Avens** (*Geum rivale*, L.), fig. 51

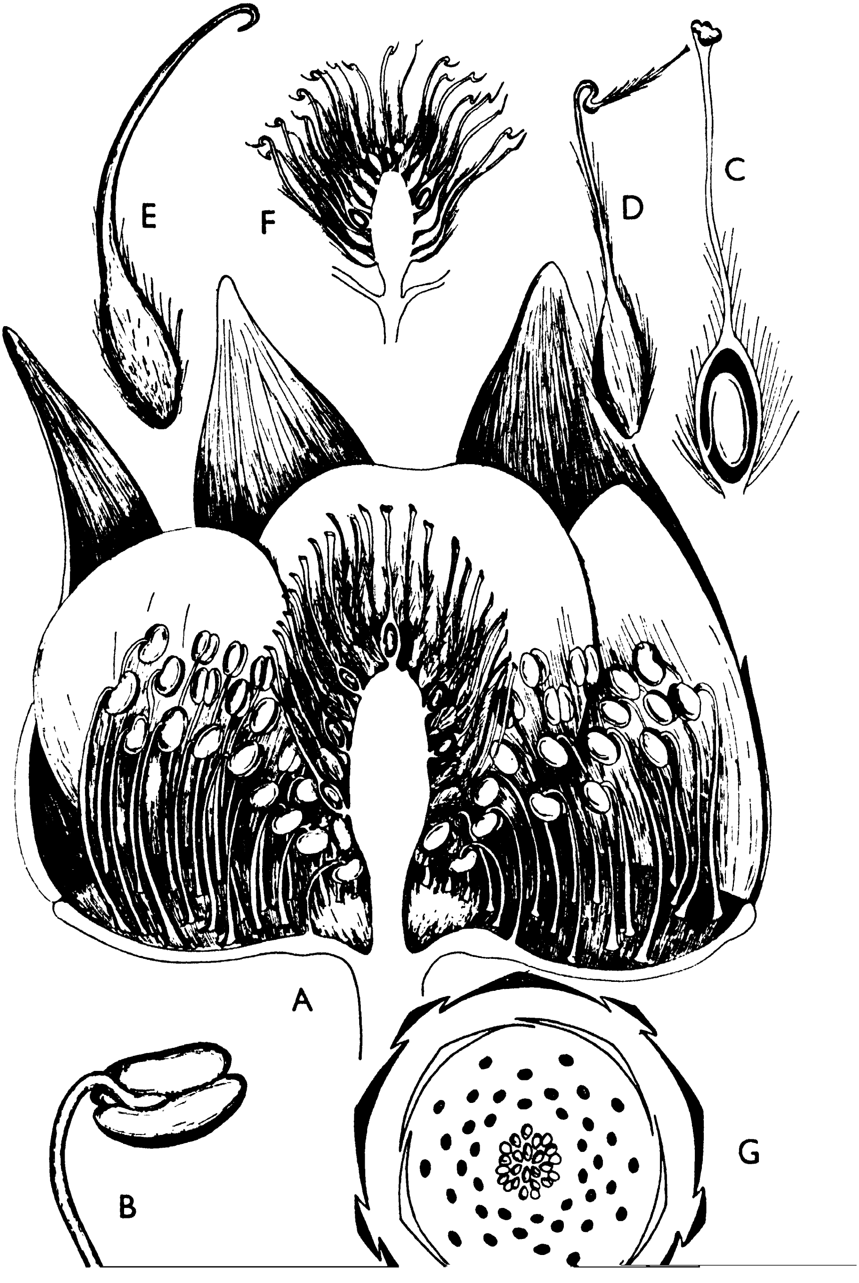
Habit: a herbaceous perennial; in damp woods and on banks of streams and ditches; flowering from May to July.

Inflorescence: the flowers arise singly in the axils of the upper reduced leaves; the mature flowers droop on long erect peduncles.

Flower: actinomorphic; bisexual; perigynous; the receptacle, as in the Blackberry, is concave with a central cylindrical portion bearing the numerous carpels.

Calyx: sepals five, alternating with five smaller members forming

Fig. 51. *Rosaceæ. Geum rivale.*—A median section, petals shorter than sepals note epicalyx cut on right. B stamen with versatile anther. C carpel and long hairy style. D fertilized carpel with apical part of style bent back. E achene fruit with terminal part of style broken off, leaving the tip as a recurved hook. F compound fruit of achenes. G floral diagram; floral formula, $K_{5+5\ \text{epicalyx}}C_5A_\infty G_\infty$.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an epicalyx which consists of the connate stipules of neighbouring sepals.

Corolla: of five free petals, rather erect in the flower; purple or tinged with orange.

Andrœcium: stamens numerous in several whorls all over the surface of the concave part of the receptacle, not confined to the outer edge as in the Blackberry; the outer stamens have taller filaments than the inner; the anthers are versatile and nod towards the centre of the flower; dehiscence is introrse.

Gynœcium: numerous free carpels, superior, confined to the central axial part of the receptacle; the carpels are prolonged into long hairy styles which terminate in recurved hooks; each ovary is unilocular and contains two ovules.

Pollination: the flowers are protogynous; the styles are taller than the stamens and when the drooping flowers are visited by bees cross-pollination is effected, as the exposed stigmas are the first parts to be touched. Later, the anthers become elevated above the stigmas by elongation of their filaments and self-pollination at this time is also probable.

Fruit: compound, consisting of a large number of hairy achenes with persistent styles which become stiff and hooked; they catch in the coats of passing animals, and may thus be dispersed.

Type 4. **The Sloe** or **Blackthorn** (*Prunus spinosa*, L.), fig. 52

Habit: a shrubby perennial furnished with spines; in hedges and thickets; flowering in March and April, before the unfolding of the leaves.

Inflorescence: cymose, resembling umbels, at the end of dwarf shoots; the older flowers are in a group at the centre with the younger flowers attached slightly below, thus forming a cymose cluster; some dwarf shoots may bear only single flowers.

Flower: actinomorphic; bisexual; perigynous; the receptacle is cup-shaped, but without the central protuberance of the previous types. The receptacle does not remain after the fruit is formed.

Calyx: five free sepals, on the outer margin of the cup.

Corolla: five free, white petals, incurved at the apex; attached to the receptacular rim within and alternating with the sepals.

Fig. 52. *Rosaceæ. Prunus spinosa.*—A, inflorescence at end of a dwarf shoot. B flower from above. C median section; note the two whorls of stamens and the single carpel—unilocular ovary with two ovules (one showing). D drupe. E floral diagram; formula, $K_5C_5A_\infty G_1$.

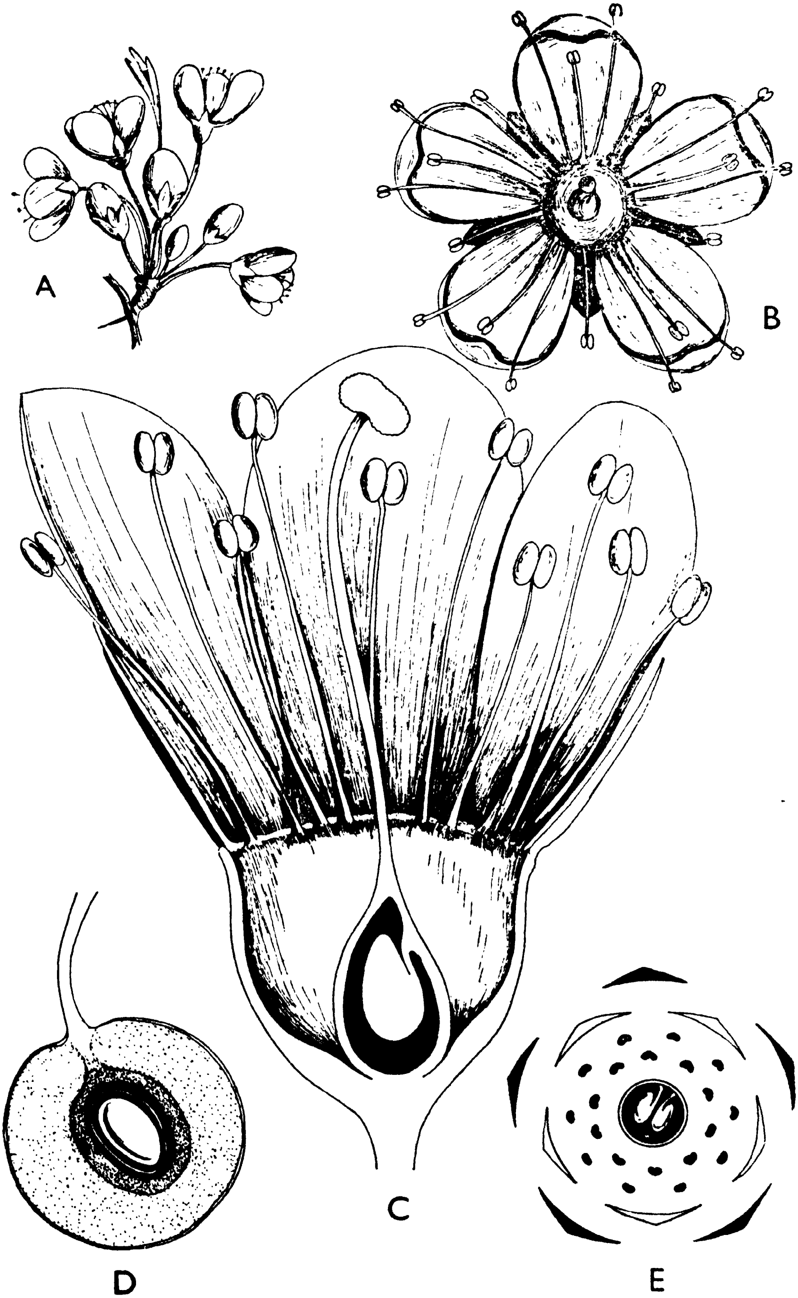

Fig. 52. (For description, see opposite)

Andrœcium: about twenty stamens, in two whorls of ten each; the outer whorl stands in five pairs opposite the five petals and those of the inner whorl alternate with them, on the inner margin of the cup.

Gynœcium: a single carpel at the base of the cup; the style ends in a broad papillose stigma; the ovary is unilocular with two anatropous ovules in pendulous placentation.

Pollination: the flowers are protogynous; they are visited for pollen and nectar, which is secreted by the inner surface of the lower parts of the receptacular cup. When the flowers first open the stamens are curved strongly inwards, so that the anthers are actually enclosed within the cup (see fig. 9). At this stage the prominent stigma is the first part to be touched by the visiting insect and cross-pollination may be effected. In older flowers the anthers are pulled out of the cup-receptacle by the elongation of their filaments. The stamens then diverge widely, the outer ones being the first to shed their pollen, followed by the inner ones; insects visiting the older flowers will thus be dusted over with pollen, but even at this later stage the style may increase in length to avoid contamination with self-pollen. If cross-pollination fails the style may curve over to allow the stigma to touch the anthers.

Fruit: a succulent drupe, covered with a bluish waxy bloom.

Type 5. The Apple (*Pyrus Malus*, L.), fig. 53

Habit: the "crab-apple" tree grows in hedges and woods; in flower during April and May.

Inflorescence: an umbellate cyme.

Flower: actinomorphic; bisexual; epigynous; the urn-shaped receptacle has closed over and combined with the walls of the carpels.

Calyx: five sepals, free, covered with a fine down, on the outer edge of a shallow cup surmounting the ovary.

Corolla: five free, pink or white waxy petals, alternating with the sepals on the edge of the epigynous cup.

Andrœcium: numerous stamens, in several whorls of ten, on the inner edge of the cup; the ten stamens of the outer whorl stand in five pairs opposite the five petals and the remaining stamens follow in regular alternation. In young blossom the anthers are incurved.

Gynœcium: five carpels, syncarpous, joined by their dorsal walls to the tissues lining the receptacular cup, thus rendering the carpels *inferior*. The five carpels are joined in axile placentation but the

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Fig. 53. *Rosaceæ. Pyrus Malus.*—A, median section; note inferior ovary. B transverse section of ovary, showing axile placentation. C, D sections of pome. E floral diagram; floral formula, $K_5C_5A_\infty G_{(\bar{5})}$.

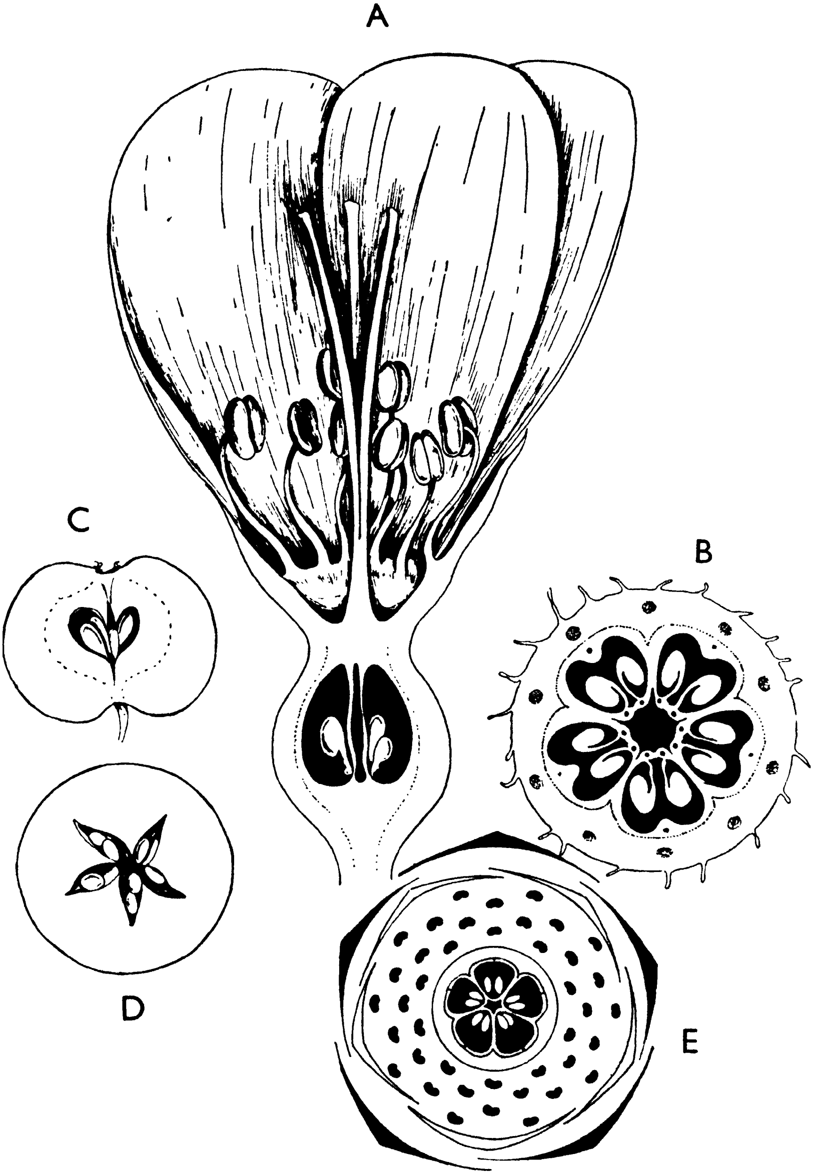

Fig. 53. (For description, see opposite)

ventral sutures fuse short of the centre, leaving a hollow in the middle of the ovary. Each loculus of the five-chambered ovary usually contains two ovules; the five styles, free distally, are fused for a short distance above the ovary.

Pollination: the flowers are protogynous. Nectar is secreted by the lining of the shallow epigynous cup. When the blossoms open, the stigmatic tips of the five styles are exposed above the level of the stamens. At this time the stamens are unripe and their filaments are incurved so that the anthers are closely crowded around the styles. When the flowers open out wider, the outer stamens straighten and diverge before liberating their pollen, and the same process is followed later by the remaining stamens. Insects coming from the older flowers will effect cross-pollination of freshly-opened flowers. Self-pollination may also take place in older flowers when the styles themselves curve outwards to touch the anthers. Several cultivated varieties of apples (and pears) possess a high degree of infertility (see Chap. XIII, p. 138), and in orchards it is advisable to interplant different varieties of apples to ensure fertilization.

Fruit: a characteristic type known as a pome (see Fruits, p. 99). During its formation, the carpellary walls become greatly toughened and form the familiar " core " which is the equivalent of the endocarp of the drupaceous " stony " fruit; within the endocarp are the brownish seeds or " pips ". The tissues of the receptacular cup with which the carpels are fused are greatly stimulated to growth after pollination, and the radial walls of the carpels become wedged apart by the intrusion of receptacle tissue, giving the appearance, in a transverse section of the fruit, of five carpels being free. The tissue becomes juicy and succulent. The smooth round fruit may be scattered in strong wind; fruit-eating animals may swallow the seeds without injury to the toughened testa.

FAMILY 9. UMBELLIFERÆ

Herbaceous plants with hollow stems and a remarkable variety of foliage; leaves often greatly dissected with broad sheathing petioles. The family includes annual, biennial, and perennial plants. It contains such economic plants as the Carrot (*Daucus Carota*), Parsnip (*Pastinaca sativa*), Parsley (*Carum Petroselinum*), Celery (*Apium graveolens*), Caraway (*Carum Carvi*), Coriander (*Coriandrum sativum*). Some species are poisonous, e.g. Hemlock (*Conium maculatum*), Dropwort (*Œnanthe* spp.). Other common plants are: Beaked Parsley, Chervil, Wood Sanicle, Pignut, Sweet Cicely, Angelica, Cow Parsnip. The plants are generally strongly aromatic, yielding ethereal oils, balsams, resins,

&c. The inflorescence is very characteristic, being a simple or compound umbel, with or without an involucre; the outer florets are often staminate or sterile and slightly zygomorphic. In development, the stamens appear first, then petals and sepals; the latter are only slightly indicated; there is a prominent glandular epigynous disc.

Type. **The Beaked Parsley** (*Anthriscus sylvestris*, Hoffm.), fig. 54

Habit: a perennial herb; in hedges and borders of fields; in flower from April to June.

Inflorescence: a compound umbel, of about six to ten simple umbels (rays); there is no general involucre below the whole umbel, but each ray has a partial involucre or involucel consisting of about six greenish bracts.

Flower: small white, mostly bisexual; slightly zygomorphic, owing to the outermost petal being larger than the others.

Calyx: no apparent sepals, these being represented by an uneven ridge at the upper limits of the inferior gynœcium.

Corolla: five free petals of unequal size; the outwardly directed anterior petal is larger than the rest; all the petals are slightly notched.

Andrœcium: five stamens, with incurved filaments, alternating with the petals and inserted on the rim of the inferior ovary.

Gynœcium: two carpels, syncarpous, inferior; one carpel faces the centre and the other the outside of the umbel. The carpels are surmounted by a shiny glandular nectary-disc out of which grow two horn-like divergent styles; in the young bud the two styles are crossed or incurved. The ovary is bilocular and each chamber contains a single anatropous ovule in pendulous placentation. The ovary is perfectly smooth and there are no oil glands (vittæ) in the ovary wall.

Pollination: the flowers are often andro-monœcious, i.e. both bisexual and staminate flowers are present. They are strongly protandrous. Frequently the central and the outermost flowers are bisexual and the rest staminate (fig. 54, B). The flowers, though individually small, are conspicuous because of their close umbellate arrangement. They are visited by a large variety of short-tongued insects, such as beetles and flies, to which the openly exposed nectar disc is easily accessible. Cross-pollination is favoured by well-marked protandry, for the stamens usually shed their pollen while the two stigmas are unreceptive and infolded (fig. 54, E). Later, the styles curve outwards to receive pollen. Self-pollination is also possible if the anthers still contain pollen at the time when the styles are divergent, in which case pollen falls on to the stigmatic surfaces.

Fruit: a smooth-walled schizocarp called a cremocarp. At maturity it splits into two one-seeded portions each called a mericarp. The fruit splits in such a way that each mericarp is attached to the ovary by a slender portion of the axis called a carpophore. The one-seeded mericarps, being thin and dry, are easily removed from their carpophores and dispersed by wind.

In the schizocarp of the Cow Parsnip (*Heracleum Sphondylium*), there are black, elongated oil glands or vittæ in the pericarp wall (fig. 54, H). Each mericarp is winged for wind dispersal.

FAMILY 10. PRIMULACEÆ

This family consists of annual or (mostly) perennial herbs with vegetative propagation by rhizomes and corms. Many species are short-stemmed rosette plants, others are compact Alpine or Arctic forms. The commoner British species are Loosestrife, Creeping Jenny, Bog Pimpernel, which grow in peaty bogs, *Hottonia* (Water Violet), an aquatic plant with finely divided leaves, Brookweed and Sea Milkwort in damp ground near the sea, and Scarlet Pimpernel, a weed of cornfields. The floral members are typically five in number (pentamerous). The structure of the Primrose is fairly typical of the family; the flowers are generally dimorphic, having two forms characterized by heterostyly, one form having a long style and the other a short style, the position of the stamens differing in the two forms. There are no plants of economic importance.

Type. **The Primrose** (*Primula vulgaris*, Huds.), fig. 55

Habit: a perennial herb with radical leaves on a short rhizome; growing in woods and hedge banks; flowering from March to May.

Inflorescence: the underground rhizome puts forth a short axis which in addition to a leafy rosette bears also a number of small bracts, in the axils of which grow a few flowers; the bracts are so close to the foliage leaves that the flowers appear to arise at the centre of the rosette, but they really form a very short-stemmed umbel.

Fig. 54. *Umbelliferæ. Anthriscus sylvestris.*—A, umbel inflorescence; note absence of general involucre. B simple umbel from above, of about 12 flowers; note slight zygomorphy of corolla (largest petal to outside). C same, side view, showing involucel. D flower, side view, showing calyx reduced to a mere rim. E gynœcium of two smooth joined carpels surmounted by epigynous disc (the two horned styles here shown in a recurved or crossed condition, in a young flower). F median section; note irregular size of petals. G smooth-walled fruit (cremocarp) with median groove but no vittæ. H cremocarp of Cow Parsnip with longitudinal vittæ. I same, side view; arrow indicates line of separation into two mericarps. J split schizocarp to show carpophores. K mericarp dissected to expose single seed. L seed. M floral diagram; floral formula, $K_0C_5A_5C_{(\bar{2})}$.

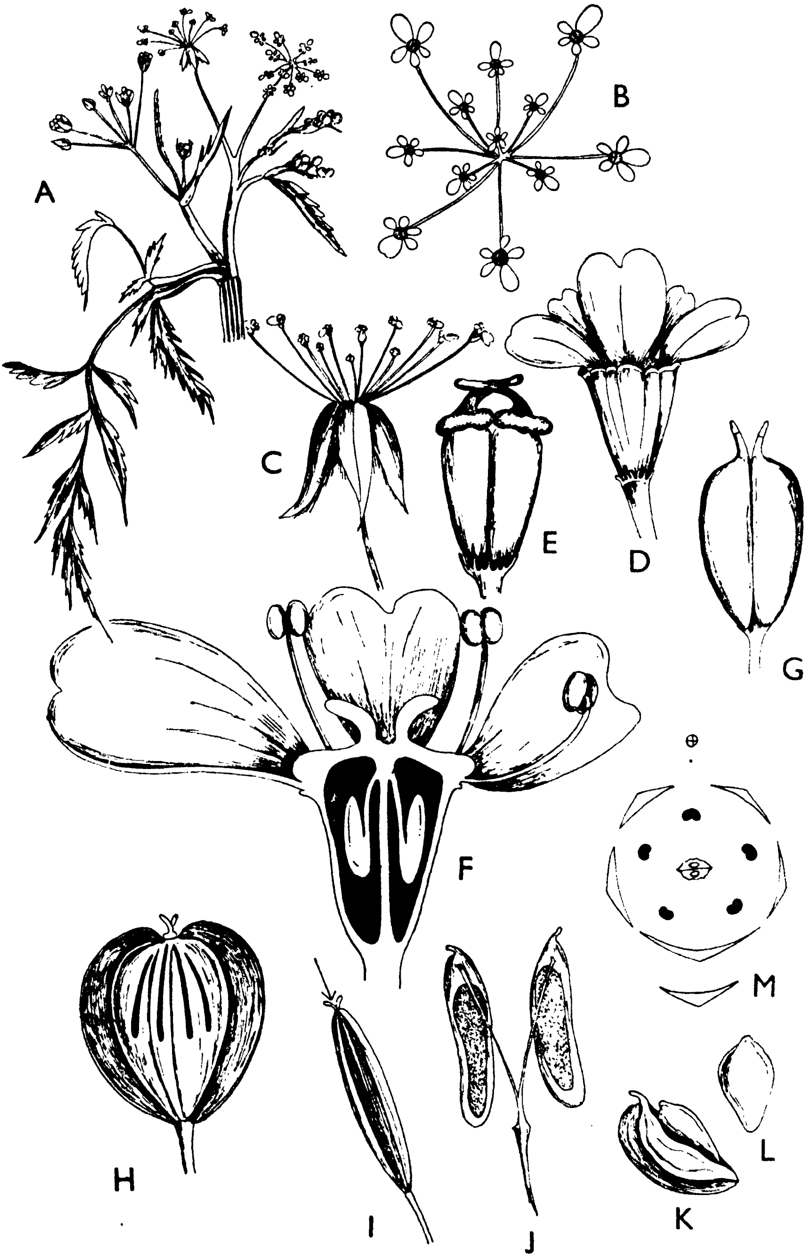

Fig. 54. (For description, see opposite)

Flowers: of two kinds (dimorphic) on distinctive plants. The two forms differ slightly in the length of their corolla tubes but markedly in the length of their styles. The long-style form has the globular stigma at the orifice of the corolla-tube and is called the " Pin-eye " kind; in the second form, the mouth of the corolla-tube is closed by the anthers, and hence it is called the " Thrum-eye " kind (from a fancied resemblance of the compacted anthers to a bunch of frayed-out threads). The flowers are actinomorphic, bisexual, and hypogynous.

Calyx: five sepals united to form a strongly ribbed tube ending in five long points.

Corolla: five yellow petals joined at their bases to form a long narrow tube which spreads out to form a five-lobed rosette; the yellow colour of the corolla merges into an orange tint around the orifice of the tube, thus forming a conspicuous " eye-spot ", attractive to insects. In the pin-eyed form the corolla tube is slightly constricted halfway down (where the stamens are inserted), but in the thrum-eyed type the constricted part and stamens occur much higher, just below the orifice of the tube. In both types of flowers the free lobes of the corolla are notched.

Andrœcium: five stamens with very short filaments; in the pin-eyed (long-style) form they are inserted halfway down the tube; in the thrum-eyed (short-style) form they are near the orifice of the tube; in both cases the stamens stand opposite to, and not in alternation with the lobes of the corolla (see fig. 16). The stamens of the Primrose are developed before the petals, which arise much later on the backs of the staminal primordia; the latter are eventually raised up by the formation of the corolla-tube, so that the stamens become epipetalous. This abnormal position of the stamens facing the petals is explained by the suppression of an outer whorl of stamens which would stand opposite the sepals. (In the Brook-weed an anti-sepalous whorl is represented by five staminodes.) The anthers have introrse dehiscence. The pollen grains of the thrum-eyed flower are considerably larger than those of the pin-eyed flower.

Gynœcium: five carpels, syncarpous, superior, forming a smooth-walled spherical ovary surmounted by a single style, which terminates in a globular papillate stigma. The size of the stigmatic papillæ differs

Fig. 55. *Primulaceæ. Primula vulgaris.*—A, the long-style (pin-eyed) flower. B short-style (thrum-eyed) flower. C median section of long-style flower. D median section of short-style flower; note relative positions of stigmas and stamens. E longitudinal section of gynœcium of long-style flower; note free-central placenta arising from base of ovary, free at its apex, and partially hollow style ending in papillate stigma. F smaller papillæ of thrum-eyed, and G coarser papillæ of pin-eyed style. H pollen grains; on left, pin-eyed, on right, thrum-eyed. I, 5-ribbed gamosepalous calyx (cf. fig. 16). J floral diagram; floral formula, $K_{(5)}[C_{(5)}A_5]G_{(5)}$.

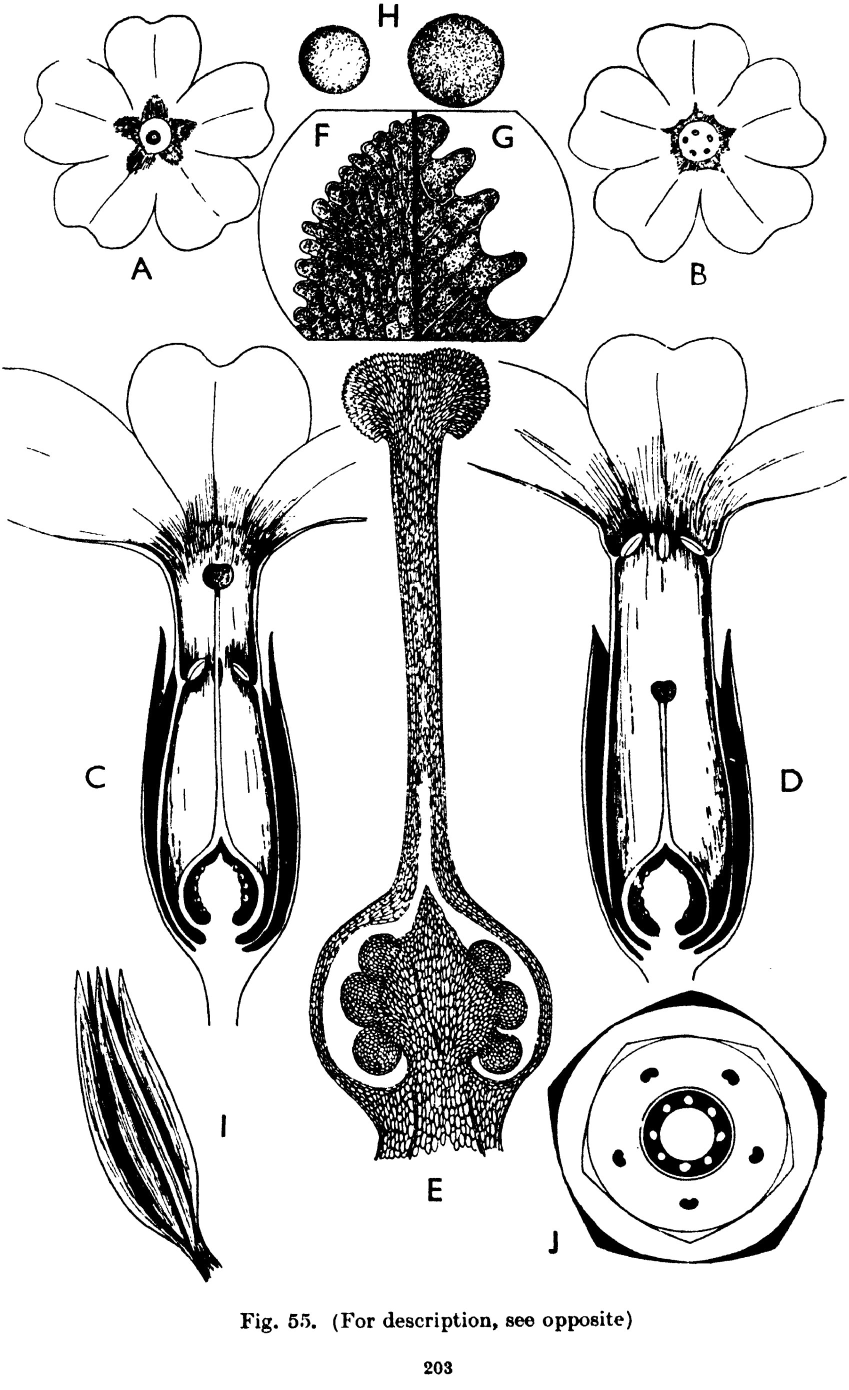

Fig. 55. (For description, see opposite)

in the two types of flowers. It is difficult to make out that there are five carpels in the Primrose, and even at its initiation the gynœcium consists of a cylindrical primordium; but a transverse section of the ovary (fig. 16) usually shows ten vascular strands (which may, however, show branching) in the ovary wall. Moreover, in abnormal flowers, the gynœcium may be entirely replaced by five leafy primordia. The fact that the fruit opens by five double teeth indicates also that this is the number of carpels composing the gynœcium.

The massive placenta arises as a solid cone of tissue from the base of the ovary and reaches almost to the base of the partially hollow style. The placenta thus bears no relation to the carpellary walls and the numerous ovules are thus said to be in free-central placentation within the unilocular ovary.

Pollination: the method of cross-pollination is correlated with dimorphism in the flowers. Nectar is secreted around the base of the ovary and is accessible only to insects with a long proboscis. The median sections of the two types of flowers should be examined side by side. It is seen that the papillose stigma in the pin-eyed type is at the same level as the stamens in the thrum-eyed form, and the stigma of the latter is at the same level as the stamens in the pin-eyed form. There is no interval of time between the maturity of the stigma and the dehiscence of anthers. If a bee visits a thrum-eyed flower first, by thrusting its proboscis deeply into the corolla tube it will pick up pollen on the basal part of its proboscis; if it next visits a pin-eyed flower, the base of the proboscis, laden with pollen, is in the right position to touch the pin-eyed stigma, thus effecting cross-pollination. In escaping from the pin-eyed flower the bee picks up pollen from the anthers at the middle of the corolla tube and therefore on the middle part of its proboscis; if it now visits the short-style, thrum-eyed flower, the stigma is exactly in the position to receive the pollen deposited on the middle part of the proboscis, so that cross-pollination is again effected. It appears that the process of selfing in either type of flower is rendered difficult on account of the relative size of the pollen grains and the spacing between the stigmatic papillæ. Microscopic examination of stigmas and pollen (fig. 55, F, G, H) shows that the short-style pistil is furnished with smaller and more densely aggregated papillæ which exactly accommodate the smaller pollen grains of the long-style flower; similarly, the larger and wider-spaced papillæ of the long-style stigma (pin-eyed) are of the appropriate size for the larger pollen of the short-style (thrum-eyed) flower. Pollinations carried out in this reciprocal fashion are known as " legitimate crosses " and they result in the production of seeds greater in number and more vigorous than if either type of flower is selfed. Despite the discrepancy in size between the pollen grains and the spacing of the stigmatic papillæ self-pollination is not entirely precluded. It is known that in the crossing between the two forms of plants the thrum-eyed condition is transmitted as a dominant Mendelian factor, so that the dimorphism of the Primrose has a genetical basis.

Fruit: a capsule dehiscing by five double teeth, with the small seeds exposed on the free-central placenta. The seeds are rich in oil (all the flower tissues possess glands containing an irritant oily substance; see fig. 16); in addition to the seeds being jerked out of the dried

Inflorescence: cymose, without bracts. The axis terminates in a flower and the succeeding flowers arise laterally as helicoid monochasia (fig. 5, O), but subsequent adhesions between the various axes often make the system complicated, particularly when some of the axes and flowers become aborted and fall off in the bud stage.

Flower: the white or violet flowers are actinomorphic (but see the orientation of the gynœcium, cut transversely in fig. 17); bisexual; hypogynous. The flowers are frequently sterile owing to incompatibility (p. 138) or to lack of pollen.

Calyx: green, hairy and persistent, consisting of five joined sepals.

Corolla: five white or violet petals, sympetalous, forming a shallow, bell-shaped (campanulate) corolla. The pointed lobes alternate with those of the calyx. During the day the flower is fully expanded and the corolla assumes an almost vertical position.

Andrœcium: five stamens, alternating with and inserted on the petals at the junction of the spreading lobes and the narrow funnel-shaped part of the corolla. The staminal filaments are very short and stout; the anthers long, cylindrical, slightly adherent, tapering and leaning towards the style, which they closely invest, so that they appear as a yellow cone at the centre of the flower, contrasting sharply with the white or purple of the corolla. Pollen-discharge takes place by small slits or pores at the tips of the anther lobes.

Gynœcium: two carpels, syncarpous, superior; they are arranged *obliquely* to the median plane of the flower. The dark-green and globular ovary terminates in a long sinuous style. The bluntly cone-shaped stigma is slightly bilobed at the base and is carried beyond the apex of the anther cone. The ovary is bilocular and the ovules are numerous on a massive axile placenta. (In other forms, as in the Tomato, the ovary becomes spuriously quadrilocular owing to the development of an additional septum; see fig. 56, G.)

Pollination: around the base of the ovary and extending almost to the level of insertion of the stamens, the surface of the corolla forms a secretory tissue. The firm and stout filaments closely invest the nectar-producing area, and insects which would reach it must force the adherent anthers apart. The prominence of the papillate stigma above the anthers ensures that it is the first part to be touched by a visiting insect, so that cross-pollination is effected; but self-pollination is also accomplished, especially at night when the flowers are partially closed, for

Fig. 56. *Solanaceæ. Solanum tuberosum.*—A, cymose inflorescence. B flower in side view; note cone of anthers. C actinomorphic corolla. D median section. E convergent anthers and protruding stigma; note apical pores for pollen discharge. F floral diagram; note oblique placenta; cf. fig. 17. G transverse section of berry of Tomato. Floral formula, $K_{(5)}[C_{(5)}A_5]G_{(2)}$.

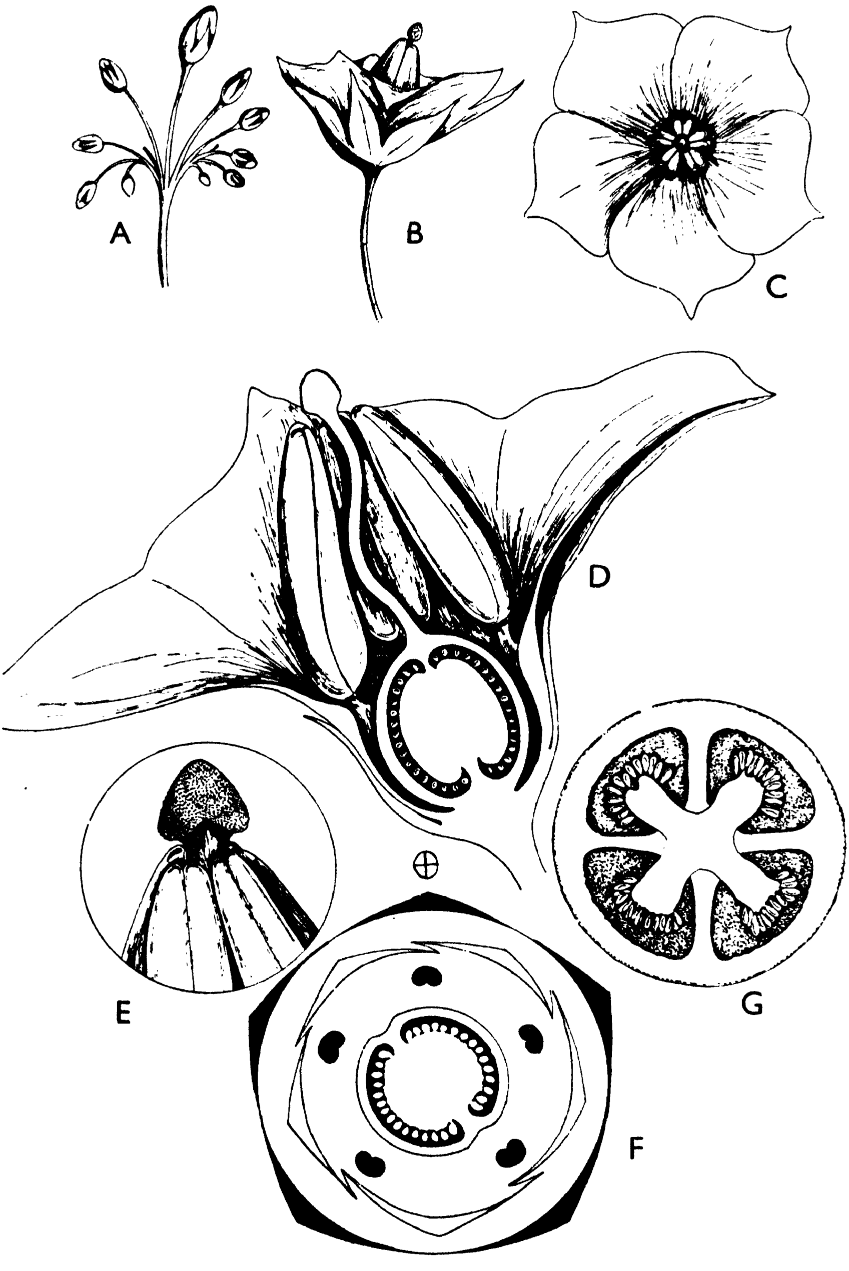

Fig. 56. (For description, see opposite)

pollen then collects within the creases of the closed corolla and may thus come into contact with the stigma. Self-pollination may also result from a continuance of growth in the funnel part of the corolla, so that towards the end of the flowering period the staminal filaments are strained and the apices of the anthers are brought into contact with the stigma. The flowers of some potato varieties are often destitute of pollen or sterile to their own pollen.

Fruit: a green berry, seldom formed (a more familiar example of the berry fruit is the Tomato, which in transverse section (fig. 56, G) appears to be quadrilocular, owing to the development of an additional septum; the thick axile placenta is deeply four-lobed).

FAMILY 12. LABIATÆ

Herbs or shrubs, with four-sided stems and opposite pairs of simple leaves. Vegetative propagation by stolons is very common. Some forms are xerophytic with small inrolled and hairy leaves. Many species contain scented and volatile oils within a glandular epidermis, e.g. Lavender (oil of lavender being obtained by the distillation of the flowers of *Lavandula vera*), Thyme (*Thymus vulgaris*), Rosemary (*Rosmarinus officinalis*), Mint (*Mentha viridis*), Peppermint (*Mentha piperita*), Sage (*Salvia officinalis*), Marjoram (*Origanum vulgare*). The commoner British types include various species of Mint, Ground-Ivy, Self-heal, *Stachys* (Woundwort, Betony, &c.), Hemp-nettle, Wood-sage and Bugle.

The inflorescence is very characteristic and is usually cymose; the flower-clusters often appear in apparent whorls (verticillasters) in the axils of opposite leaves. Floral structure is very constant throughout the family.

Type. The White Dead-Nettle (*Lamium album*, L.), fig. 57

Habit: a perennial herb; under hedges and banks; the flowering period usually extends from May to September.

Inflorescence: there is a pair of inflorescences at each node, one in the axil of each foliage leaf. If a young inflorescence towards the apex

Fig. 57. *Labiatæ. Lamium album.*—A, the plant showing the verticillaster inflorescences in the leaf axils. B a plan of a verticillaster in relation to the square stem. C ditto, to show, in conventional form, the cymose derivation of each half of a verticillaster. D the bilabiate flower, in front view. E upper part of corolla cut away to show the 2 long and 2 short stamens, with bearded oblique anthers. F median section of a flower. G fruit (carcerulus) of four nutlets within the five-toothed calyx. H the floral diagram; floral formula, $K_{(5)}[C_{(5)}A_{2+2}]G_{(2)}$.

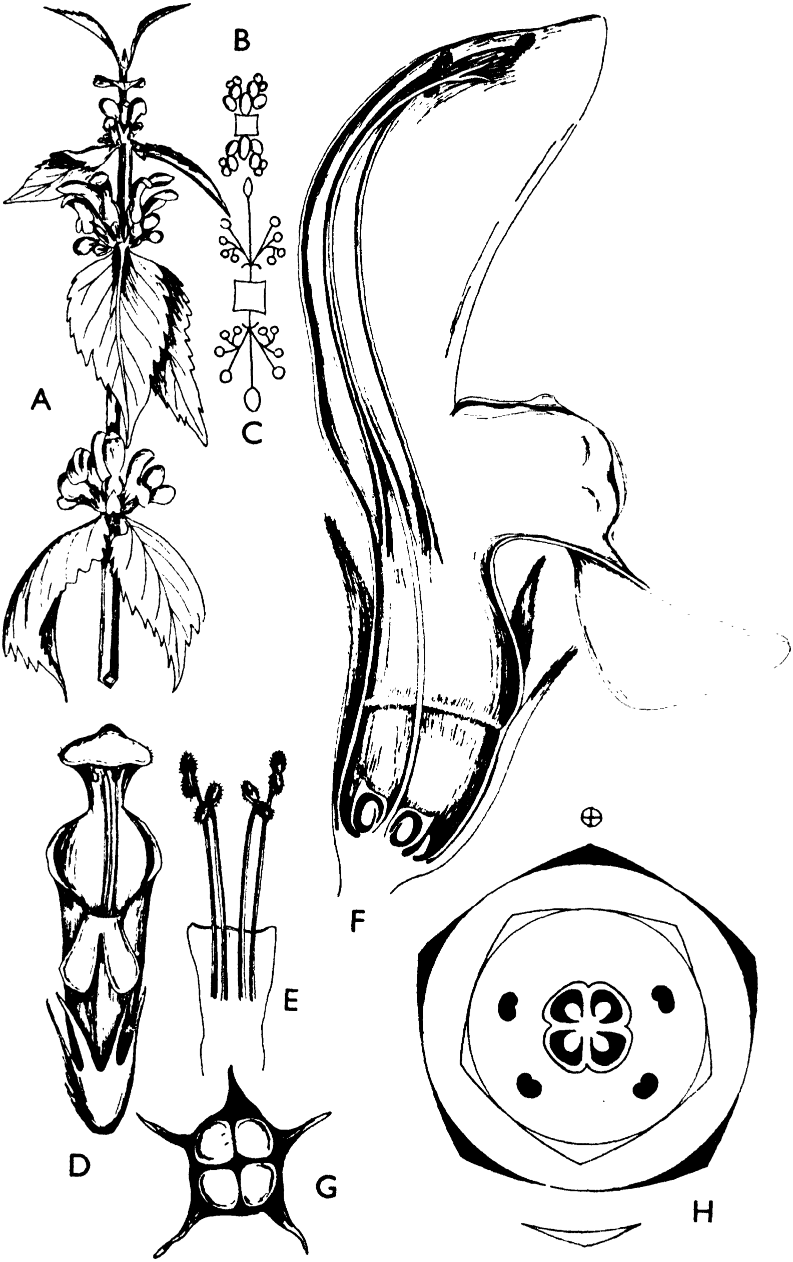

Fig. 57. (For description, see opposite)

of the plant is examined from above, it is seen that on two sides of the square stem there is a group of flowers arranged in the form of a condensed dichasium. Eleven flowers is a common number in such a group; of these, one is terminal on a very short axis in the axil of the foliage leaf, and in the axils of the prophylls on this axis arise the next two flowers, the system thus far making a dichasium; the axes of these two lateral flowers, in turn, give rise each to a monochasial system made up, usually, of three or four flowers, and the paired system, at each node, is called a verticillaster (fig. 57, B & C). In a fully opened system the terminal and oldest flower stands directly above the leaf, and the next older flowers form a pair, one on each side, the younger flowers then following in monochasial arrangement.

Flower: strongly zygomorphic in the median plane; bisexual; hypogynous.

Calyx: tubular, gamosepalous; the five sepals project as finely pointed and hairy teeth.

Corolla: of five petals. sympetalous; the tubular basal portion is narrow; in this part, as seen in a median section of the flower, there is a ring of hairs about halfway up the tube and above this zone the tube expands anteriorly; the tube is continued above into an erect hood beneath which the stamens are protected; the hood represents two fused petals; the two lateral petals at the base of the hood are rather ill-defined but can be distinguished by their slightly projecting narrow lobes; the drooping part of the corolla, forming a lip, is deeply notched and represents the fifth anterior petal. The whole corolla may be described as bilabiate, the posterior hood forming an upper lip and the lateral petals together with the anterior petal making a lower lip, the whole forming a typically zygomorphic corolla.

Andrœcium: four stamens, epipetalous, facing the sepals; there is no stamen opposite the posterior sepal. Two of the stamens with long filaments are in front, facing the anterior sepals; the shorter pair is behind the taller and stands opposite the lateral sepals. The anthers are fringed with hairs and their lobes are widely divergent.

Gynœcium: two carpels, syncarpous, superior. When the corolla is removed, the ovary will be seen at the bottom of the tubular calyx as four small green lobes, from *between* which the style arises (*gynobasic*). Two of these lobes are formed from the anterior carpel and two from the posterior one owing to the division of each carpel by a septum; each of the four lobes encloses a single ovule. The style terminates in a forked stigma.

Pollination: the flower is pollinated by humble-bees which obtain nectar from a ridge of tissue situated at the basal anterior edge of the ovary. Alighting on the lower lip, the insect in forcing its head down the corolla brings its back into contact with the projecting anthers, which face downwards; at this time the style, with its stigmas closed, is pressed against the posterior hood, and is thus out of reach of the insect. When the insect visits an older flower, the style has moved forward and is now in the correct position for its open stigmas to pick up pollen from the insect's back. Self-pollination may also be possible when the insect withdraws from the flower, or, as often happens, when the style curves inwards so as to come into contact with the anthers. The ring of hairs inside the corolla tube protects the nectar from small creeping insects which would be of no service in pollination.

Fruit: the four lobes of the ovary separate in the fruit as small one-seeded nutlets; the whole fruit is a schizocarp called a carcerulus. The nutlets are very hard and smooth; they are easily ejected from the calyx-tube when the dried wiry stem of the plant sways in the wind.

FAMILY 13. SCROPHULARIACEÆ

Mostly annual and perennial plants, including a number of semi-parasites. The Eyebright (*Euphrasia*), Yellow-rattle (*Rhinanthus*), Lousewort (*Pedicularis*), and Cow-wheat (*Melampyrum*), are common weeds in pastures, and are partial parasites on the roots of grasses. Other common British plants are: Foxglove (*Digitalis*), Snapdragon (*Antirrhinum*), Figwort (*Scrophularia*), Monkey-flower (*Mimulus*), Toadflax (*Linaria*) and Speedwell (*Veronica*), the latter with a wide range of species thriving in various habitats. *Pentstemon* and *Calceolaria* are common cultivated forms.

Many genera contain poisonous plants, the best-known being the Foxglove, which yields the drug digitalis. The flowers are generally zygomorphic and there is an interesting "reduction series" in the number of stamens, exemplified by Mullein (*Verbascum*) with a complete complement of five; Figwort (*Scrophularia*) with four, plus a posterior staminode; Foxglove (*Digitalis*) with four, the typical number for the family, and finally Speedwell (*Veronica*), which has only the two post-lateral stamens present.

Type 1. The Foxglove (*Digitalis purpurea*, L.), fig. 58

Habit: a perennial herb, in woods, at roadsides, &c., flowering from June to August.

Inflorescence: a typical raceme. The racemes may be terminal on the main axis or on short lateral branches. The unilateral position of the flowers on the raceme is assumed during development. Each flower arises in the axil of a short leafy bract, and as development proceeds its pedicel elongates and may become curved, so that all the flowers face outwards to secure the maximum area of colour for insect attraction. When fully formed the large elegant flowers hang obliquely downwards.

Flower: tubular and zygomorphic; bisexual; hypogynous.

Calyx: five smooth, green sepals, free or very slightly united at the base and usually widely spreading; the posterior sepal is smaller than the others.

Corolla: of five petals, sympetalous, taking the form of a somewhat compressed and elongated bell, constricted slightly above the base and slanting downwards and outwards from the axis of the raceme. The mouth of the tubular corolla is divided into two unequally developed lobes. Of these, the one which is the upper in the pendulous flower is really posterior. It is shorter than the lower anterior lobe, and is distinctly notched. A study of the development of the flower shows that the upper notched lip represents two posterior petals, while the longer lower lip corresponds to the other three petals. On the inner side of the protruding lip are found dark purple blotches with white margins beset with light-coloured hairs. The blotches act as " honey-guides " to nectar-seeking insects, and the hairs provide a firm foothold for the insect visitor.

Andrœcium: four stamens, epipetalous; there is no fifth, posterior stamen; two stamens with long filaments are anterior, facing the front sepals; the two shorter stamens are behind the other pair and face the lateral sepals. All the filaments are rather thick and towards the base are strongly curved inwards so as to press the anthers very close together, and into close contact with the upper side of the corolla. The two lobes of an anther are united only at the upper end, so that they diverge widely from the point of attachment to the filament (fig. 58, C and D). The anthers dehisce in an introrse manner.

Gynœcium: two carpels, syncarpous, superior; bilocular, with numerous small ovules on a thick, massive axile placenta. The style is terminal and forked at its extremity into a bilobed stigma which stands between the anthers and close to the upper wall of the corolla tube.

Pollination: the nectary consists of a yellowish annular ridge surrounding the base of the ovary. Immediately above the ridge an area of the ovary wall is beset with hairs which prevent the access of small flies to the nectar below. The flowers are protandrous. The

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Fig. 58. *Scrophulariaceæ. Digitalis purpurea.*—A, simple racemose inflorescence. B pendulous flower, in position relative to axis and bract. C andrœcium of two tall and two short stamens with divergent anther lobes; note young style, with closed stigmas, behind anthers. D stamen with divergent anther lobes. E median section. F two-valved capsular fruit. G floral diagram; formula, $K_5[C_{(5)}A_{2+2}]G_{(2)}$.

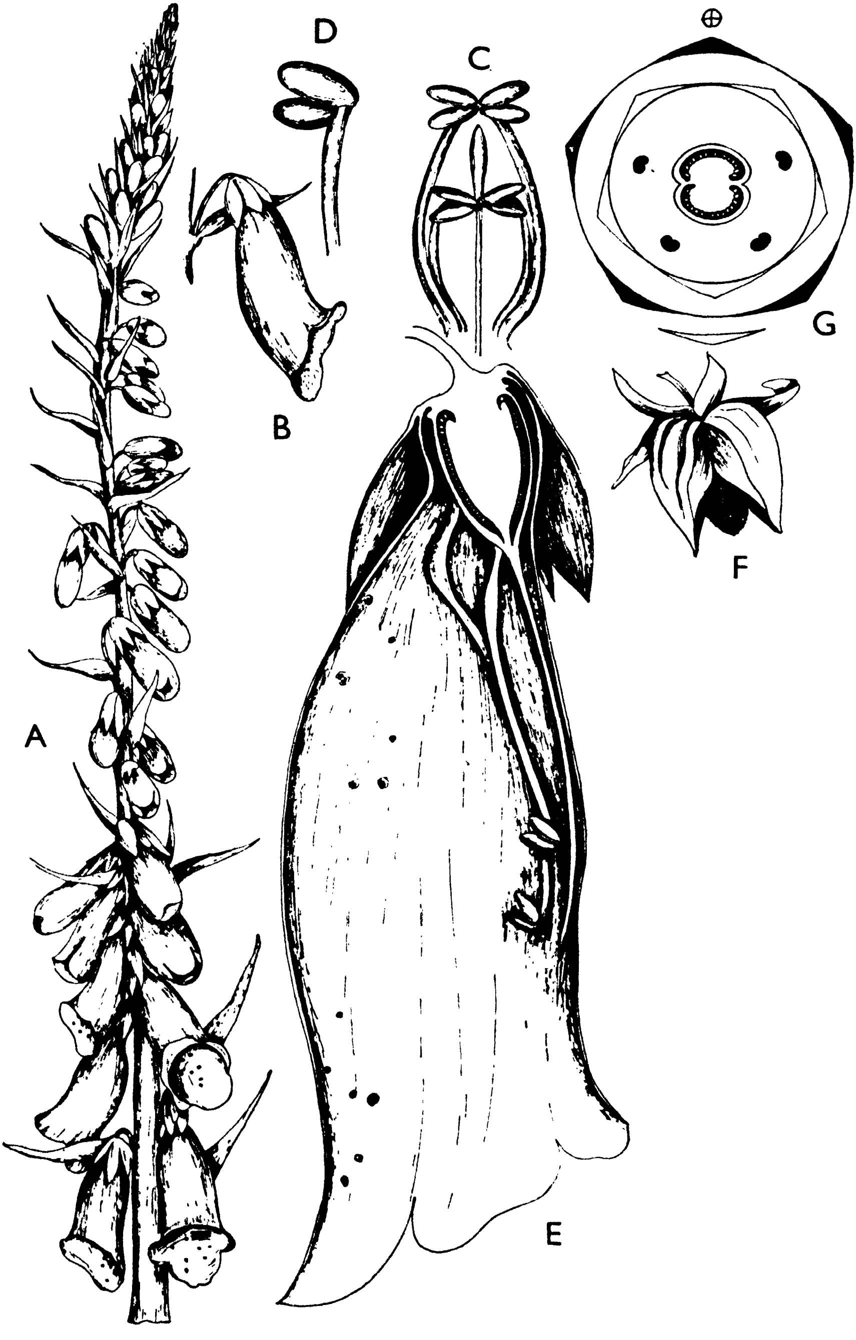

Fig. 58. (For description, see opposite)

anthers of the longer stamens dehisce before those of the shorter stamens, but these also shed their pollen before the stigma is receptive. Meanwhile the lobes of the stigma remain closed, and the style is pressed hard against the upper wall of the corolla-tube until the pollen is shed. The pendulous flowers, all turned towards the light, present an attractive mass of colour, and are visited chiefly by humble-bees. The body of the insect fits closely into the corolla and while it is probing for the nectar which collects within the constricted base of the corolla tube, its back gets dusted over with pollen. At this time the style is in close contact with the corolla tube and is not touched by the escaping insect. In older flowers the style leans forward into the tube and the stigmatic lobes diverge widely; they occupy a position corresponding to that which the anthers take up in freshly-opened flowers. At this later stage the stigmas are right in the path of the pollen-laden insect and the receptive tips of the stigmas are in the right position to pick up pollen from the insect's back; thus cross-pollination is effected. Self-pollination is not entirely prevented, for in the second stage pollen may drop on to the stigmas, which are then close up to the anthers.

Fruit: a capsule, permanently enclosed in the calyx. It opens along the two ventral sutures and the margins of the septum break across, so that when the two valves gape open the very numerous small seeds can be seen on the cone-shaped placenta. The seeds are scattered when the plant is shaken by the wind.

Type 2. The Figwort (*Scrophularia nodosa*, L.), fig. 59

Habit: a herbaceous perennial with a square axis and a tuberous underground stem; on the borders of woods and waysides; flowering from June to September.

Inflorescence: mixed; the main axis is indefinite, but in the axils of opposite pairs of foliage leaves the flowers are arranged in dichasial cymes; the latter are often incomplete, i.e. one of a pair of lateral flowers may be completely suppressed or represented by a small abortive bud; or a single flower may replace a whole dichasium.

Flower: zygomorphic; bisexual; hypogynous.

Fig. 59. *Scrophulariaceæ*. A to F. *Scrophularia nodosa*.—A, "mixed" inflorescence; racemose central axis bearing lateral pairs of axillary cymes. B corolla cut open, exposing four stamens and posterior staminode. C median section of flower at first stage of pollination; note incurved immature stamens and protruding stigma. D median section of flower after pollination; note erect anthers and withdrawal of style. E ripe capsule, F floral diagram; floral formula, $K_{(5)}[C_{(5)}A_{4+\text{staminode}}]\underline{G}_{(2)}$.

Veronica Chamædrys.—G racemose inflorescence. H flower, showing deeply-cleft corolla of 4 petals; note the two stamens widely divergent laterally, and forward projecting style.

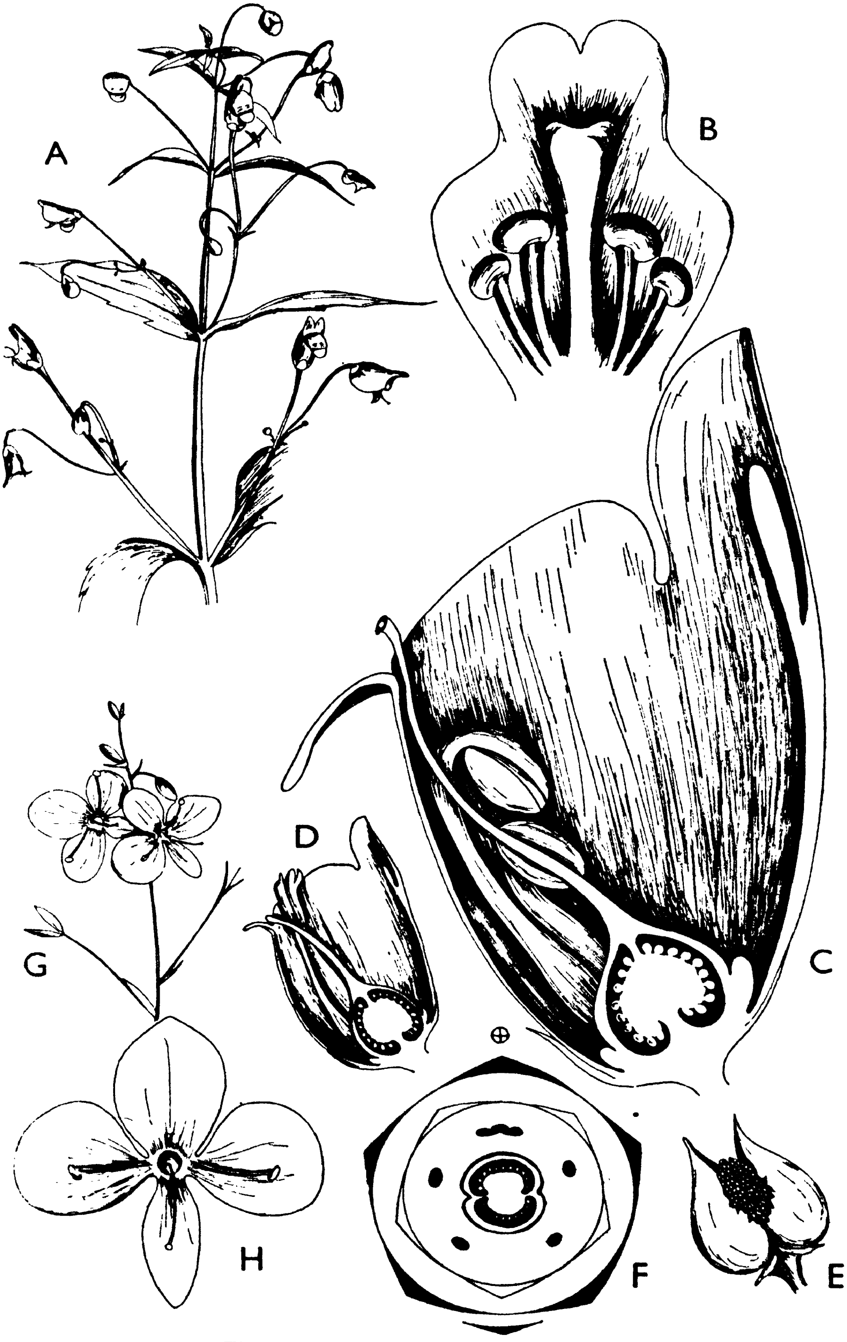

Fig. 59. (For description, see opposite)

Calyx: five sepals, gamosepalous, five-lobed.

Corolla: five petals, brownish-green, sympetalous, broadly tubular or cup-shaped, the posterior part erect and bilobed, the anterior portion projecting outwards and downwards as a drooping lip.

Andrœcium: four stamens and a staminode, epipetalous; the two anterior stamens are slightly taller than the posterior pair; in the earlier stages of flowering, the stout filaments of the stamens are curled inwards so as to carry the broad, transversely attached anthers almost to the base of the corolla-tube. The position of a fifth posterior stamen is occupied by a prominent brown-coloured, wedge-shaped staminode which is joined to the corolla-tube for about two-thirds of its length from the base, the free part above being slightly bilobed.

Gynœcium: two carpels, syncarpous, superior; the ovary is bilocular with numerous ovules in axile placentation. The style curves forward, resting against the anterior part of the corolla tube, above which it projects during the earlier stage of flowering, thus exposing the small papillose stigma.

Pollination: the Figwort is pollinated by wasps. The flowers are strongly protogynous. The flowers emit an unpleasant odour and nectar is secreted copiously from a prominent ring of tissue situated around the ovary. In the earlier stages of flowering (fig. 59, C) the stigmatic tip protrudes over the anterior edge of the corolla, and the wasp, carrying pollen from an older flower on the under side of its body, thus effects cross-pollination. In the second stage of maturity (fig. 59, D), the style withdraws the stigmatic tip away from the edge of the corolla, and by this time the incurved stamens stand erect with the anthers at the mouth of the corolla tube. The anthers open by slits along their upper surfaces. It is at this stage that the wasps collect pollen. When, in the earlier part of the flowering season, the flowers are in bloom before wasps are on the wing, self-pollination may take place at the second stage of maturity, when the dehiscent anthers stand immediately above the stigma.

Fruit: a capsule, dehiscing along the ventral sutures.

Type 3. The Germander Speedwell (*Veronica Chamœdrys*, L.), fig. 59

Habit: a small herbaceous perennial, with single lines of hairs along alternate sides of the internodes; in hedge banks; flowering in May and June.

Inflorescence: a single axillary raceme of a few light-blue flowers.

Flower: zygomorphic; bisexual; hypogynous.

Calyx: four sepals, gamosepalous; a fifth posterior sepal is suppressed.

Corolla: zygomorphic, sympetalous, blue, very deeply four-lobed and spreading; the large posterior lobe consists of two fused petals; all the petals are marked with "honey-guides" converging towards the small and shallow tube at the centre of the corolla.

Andrœcium: only the two posterior-lateral stamens are present; they are epipetalous on the throat of the corolla tube and diverge right and left from the centre of the flower.

Gynœcium: conforms with the normal structure; two carpels, syncarpous, superior; axile placentation; the style projects forward, standing directly above the small anterior petal.

Pollination: the flowers are protogynous and are pollinated by bees and hover-flies. The nectar secreted around the ovary-base and collected within the shallow tube of the corolla is fully exposed and easily accessible. If the visitor is a bee, the insect, in alighting, first touches the projecting and receptive stigma with the underside of its body, thus effecting cross-pollination. In settling down on the flower the insect gains foothold by grasping the two stamens, right and left, thus drawing the anthers under its body; the pollen thus collected is deposited on the upturned stigma of the next flower visited. At this earlier stage of maturity, although the insect draws the anthers under its body so that it is possible for them to touch the stigma, they are not yet ripe; such marked dichogamy hinders self-pollination. In the second stage, when the anthers are dehiscent, however, deposit of self-pollen cannot be avoided. In long periods of wet weather, when the flowers hardly open and when insect visits are few, the closed petals must obviously cause the anthers to come into contact with the stigma and self-pollination is thus effected.

Fruit: a broad, flat capsule, with few but rather large seeds.

FAMILY 14. COMPOSITÆ

The largest family of Angiosperms. The great majority are herbaceous plants, shrubs and trees being comparatively rare. Their distribution in diverse habitats is world-wide and they present great variety in vegetative development. Many members of the family are of economic importance or medicinal value; they contain dyes, ethereal and fatty oils, resins, &c. Drug plants include Coltsfoot (*Tussilago*), Chamomile (*Matricaria*), Wormwood (*Artemisia*), Arnica (*Arnica montana*), and Dandelion (*Taraxacum*). Food plants include Endive (*Cichorium endivia*), Lettuce (*Lactuca sativa*), Salsify (roots of *Tragopogon*), Jerusalem Artichoke (tubers of *Helianthus tuberosus*), Artichoke (heads of *Cynara Scolymus*), and Chicory (ground root of *Cichorium*

Intybus). The commoner British or garden plants include Daisy, Chrysanthemum, Sunflower, Thistle, Cornflower, Burdock, Butterbur, Groundsel, Ragwort, Knapweed, Aster, Dahlia, Cineraria, Marigold, Hawkweed, Doronicum, and Edelweiss (Alpine). The family is easily identified by its characteristic capitulum inflorescence, the small, densely aggregated flowers being known as florets; the capitulum is surrounded by a dense array of bracts, known as the involucre. The family is divided into two groups:

1. *Liguliflorœ.* The plants of this sub-family contain a milky latex stored in special laticiferous tubes which are found in association with the phloem tissue; such a tube is a continuous system formed by the breakdown of the cross-walls between a longitudinal series of cells, and a number of tubes may anastomose. The florets are of one kind, the corolla being strap-shaped or ligulate, e.g. Dandelion.

2. *Tubuliflorœ.* There is no laticiferous system in this sub-family. The florets are mostly of two kinds, (*a*) *Ray florets*, situated around the margin of the capitulum, and ligulate; usually unisexual, carpellate, rarely neuter; and (*b*) *Disc florets*, occupying the centre of the capitulum, and tubular in shape with five petal-segments; they are usually bisexual, rarely unisexual (see *Tussilago*, below); the Daisy has both ray and disc florets of the usual types, while the florets of Groundsel are all tubular and of the disc type.

The widespread distribution and the great success of the *Compositœ* are attributed largely to their diverse methods of vegetative propagation and to the elaborate, highly effective mechanisms for ensuring cross-pollination and seed dispersal. There is considerable dimorphism in the florets; the most common condition, as in the Daisy, is that the ray florets are carpellary and the disc florets bisexual; in the Sunflower, the ray florets are neuter, serving merely for attraction, but the disc florets (with interfloret bracts) are bisexual; in the Cornflower all the florets are tubular, but the outer, attractive ones are neuter and the inner bisexual; the Butter-bur has two kinds of plants, one bearing capitula of staminate flowers only, or occasionally mixed with a few bisexual flowers, and the other of capitula which contain a far greater number of carpellary than bisexual florets. The family exhibits a high stage of evolutionary development in floral structure (see figs. 10, 20, 21, 22). Four somewhat divergent types are described below.

Type 1. **The Dandelion** (*Taraxacum officinale*, Weber), fig. 60

Habit: a perennial herb with a stout tap-root which passes into a very short sympodial stem bearing a rosette of foliage leaves; in waste places and roadsides; flowering for an extended period, usually from March to September.

Inflorescence: indefinite; a capitulum on a long stalk arising in the axil of a leaf, and consisting of numerous (about a hundred or more) florets arranged on the saucer-like expansion of the peduncle, forming a " head " or capitulum, which functions as a common " receptacle " to the numerous sessile florets. The florets are developed centripetally; the older ones are at the margin, and the younger at the centre. The peduncle is hollow and bears around the expanded head a series of bracts called an involucre, which affords a common protection to all the florets of the inflorescence; the outermost bracts are reflexed over the peduncle, but the inner ones are upright and closely invest the capitulum. The mature inflorescence opens in bright light and closes at night or in dull or wet weather; these movements are controlled by changes in tissue-turgor within the base of the inner bracts. There are no bracts between the individual florets. (Cf. Sunflower, fig. 22.)

Flower: all the florets are of one kind; the strap-shaped, ligulate corolla makes the perianth strongly zygomorphic; bisexual; epigynous.

Calyx: a circlet of fine silky hairs, called a pappus, represents the calyx. The hairs are attached below the insertion of the corolla tube, around the apex of a very short axis above the ovary. At fruiting time, this brief axis becomes greatly elongated and bears the outspread pappus at its apex and the inferior fruit at its base. The protective function of a typical calyx appears to be very efficiently discharged by the involucral bracts.

Corolla: partly ligulate and partly tubular; the distal, flat portion, yellow in colour, forms a narrow ribbon terminating in five teeth which indicate the number of fused petals; at the base it gradually passes into a short, hairy, light-coloured tube.

Andrœcium: five stamens, epipetalous by short filaments fastened within the orifice of the tubular part of the corolla, and alternating with the corolla segments. The five anthers are coherent by their margins (syngenesious) to form a hollow tube through which passes the style from the ovary below; anther dehiscence is introrse, towards the style.

Gynœcium: two carpels, syncarpous, inferior; they occupy an antero-posterior position; the ovary is broad above and covered with rows of small upwardly directed teeth. The ovary is unilocular and contains a single ovule in basal placentation. The long, hairy style passes up through the anther tube, expanding above, in the mature flower, into two stigmatic lobes which are receptive on their inner (upper) surfaces only.

Pollination: the flowers are protandrous. Nectar is secreted by a ring of tissue around the base of the style and is poured into the tubular part of the corolla; it is easily accessible to a large number of insects with long or short probosces. The florets open in centripetal order, from the margin to the centre of the capitulum. In freshly opened florets near the centre, there are no visible signs of the styles, for they are as yet short and concealed within the anther tubes; the latter, however, are filled with pollen discharged introrsely around the style. In slightly older florets the hairy styles (the hairs are known as " collecting hairs ") are elongated and during their extension the collecting hairs brush out a great quantity of pollen which adheres to them; at this stage the stigmatic lobes are closed. Insects, alighting at the centre of the capitulum, circle round and probe into contiguous florets for nectar until they finally reach the fully extended stigmas of the mature florets at the margin, which are thus pollinated. Pollination takes place when pollen is carried from one floret to another in the same capitulum or from one capitulum to another. (Presumably the latter procedure results in more vigorous seeds.) Self-pollination in a floret may occur; the two stigmatic lobes curl until contact is made with the pollen on the collecting hairs on the surface of the style.

This mechanism, with slight modifications, is common throughout the whole family of *Compositæ*, and with the marked aggregation of the flowers into showy capitula, it is a very efficient method of ensuring cross-pollination. In some species with inconspicuous capitula, e.g. the Groundsel (*Senecio vulgaris*), self-pollination is very prevalent, the divergent stigmatic lobes picking up self-pollen in the manner specified above.

Fruit: a one-seeded achene attached to an elongated axis developed above the ovary; the axis bears the divergent bristles of the pappus. The familiar " head " or " dandelion-clock " is therefore composed of a number of fruits, each the derivative of a single floret, and is an *infructescence* or the product of a whole inflorescence. The feathery achenes become raised by the " receptacle " (i.e. the capitulum) altering its shape from flat to convex; this change is brought about by growth and curving back of the basal parts of the inner involucral bracts.

Fig. 60. *Compositæ. Taraxacum officinale.*—A, closed capitulum surrounded by involucre. B median section of capitulum showing young florets at centre. C a floret. D separation of stigmatic lobes, with pollen on outer collecting hairs. E, achene fruit with pappus. F floral diagram; floral formula, $K_{pappus}[C_{(5)}A_{(5)}]G_{(\bar{2})}$.

Tussilago Farfara.—G capitulum with bracts on peduncle. H median section of capitulum; note central staminate florets surrounded by numerous carpellary florets. I ligulate ray floret; note fringed corolla-tube. J tubular floret with vestigial ovary; note fused anthers. K style of same, within anther-tube. Floral formulæ: (*a*) Ray floret, $K_{pappus}C_{(5)}A_0G_{(\bar{2})}$; (*b*) Disc floret, $K_{pappus}[C_{(5)}A_{(5)}]G_{\bar{0}}$.

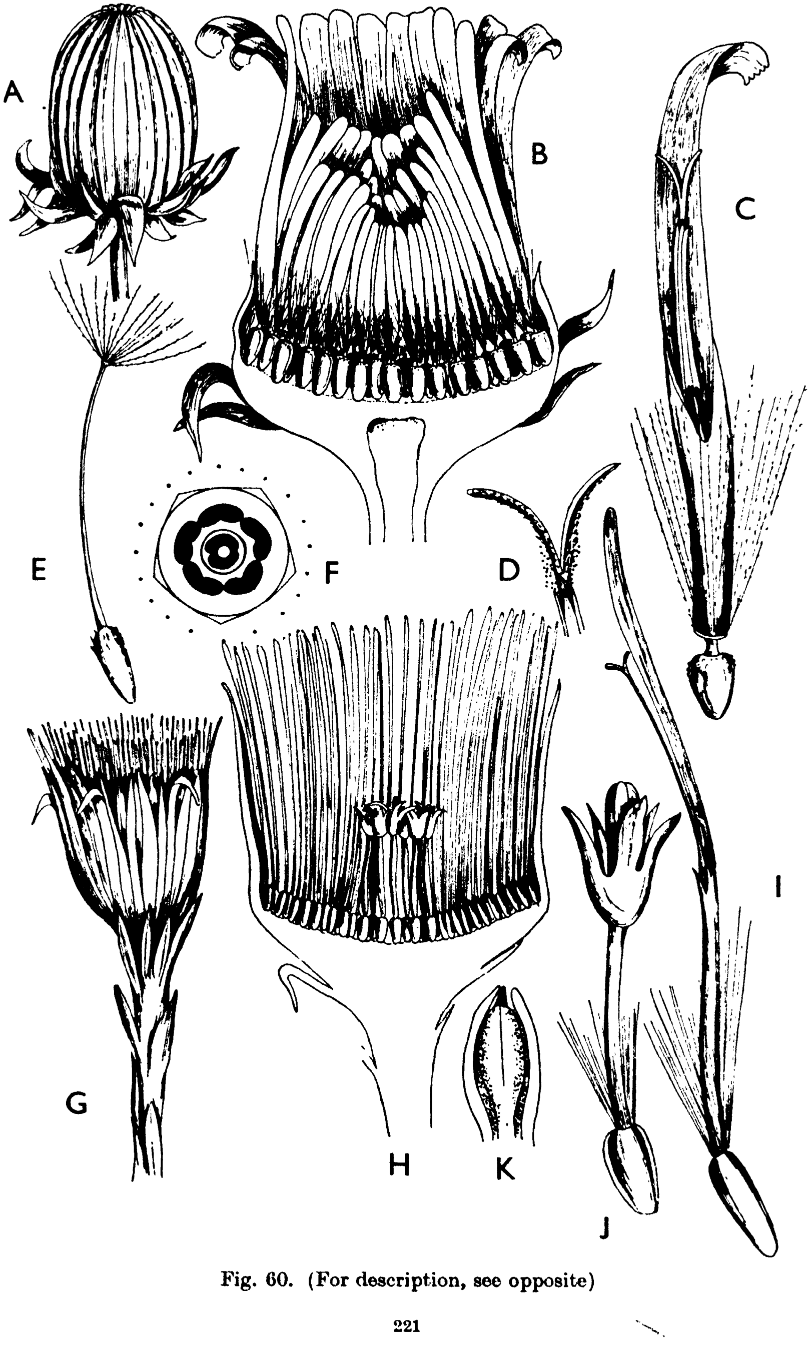

Fig. 60. (For description, see opposite)

The achenes are thus better exposed for wind dispersal, and the numerous small teeth on the pericarp, directed towards the pappus, enable the tiny fruits to catch on the ground.

Type 2. The Coltsfoot (*Tussilago Farfara*, L.), fig. 60

Habit: a perennial herb, with long, branching underground stems; flowering before the appearance of the leaves; in waste places and embankments; a troublesome weed on clay soils.

Inflorescence: a capitulum, fringed with rather long and erect bracts; the peduncle is also covered with closely-set triangular bracts. There are two kinds of florets; the outer, carpellary florets are very numerous and furnished with narrow, ligulate corollas; at the centre, the capitulum is occupied by only a few staminate tubular florets.

Flowers: (*a*) *Outer, Ray* or *Ligulate Floret*; very numerous (about 300); zygomorphic; yellow; unisexual (carpellary); epigynous.

Calyx: pappose, like that of the Dandelion.

Corolla: zygomorphic, ligulate, but there is no indication, as in the corolla of the Dandelion, of a toothed termination that would indicate the number of constituent petals; the tubular basal part of the corolla is very narrow and at its junction with the ligulate part it carries a fringe of hairs.

Andrœcium: no stamens.

Gynœcium: two carpels, syncarpous, inferior; the style has a two-lobed stigma and bears a few collecting hairs, despite the absence of anthers and pollen. There is no nectary in the floret. The ovary is unilocular and is furnished with a functional basal ovule.

(*b*) *Inner, Disc* or *Tubular Floret*; actinomorphic; yellow; unisexual (staminate); epigynous. They are very few (forty or fewer) in comparison with the ray florets.

Calyx: pappose.

Corolla: actinomorphic; a long tubular part expands into a campanulate and regular corolla terminating in five equal lobes.

Andrœcium: of five stamens, with the anthers fused to form an anther tube, within which is a style bearing the usual collecting hairs.

Gynœcium: there is an apparent ovary surmounted by a hairy style, but the ovule is abortive, and the florets are thus virtually staminate. There is a yellow nectary ring around the base of the style.

Pollination: in a particular capitulum, the outer carpellary florets are receptive to pollen several days before the staminate florets shed their pollen; the necessary pollen must therefore be conveyed by insects from other and older capitula in which the staminate florets are at the pollen-shedding stage. The Coltsfoot has a long flowering season, so that there is ample opportunity for cross-pollination between different capitula to take place. Within the same capitulum, however, pollination must obviously take place on a wide scale, in the following way. When the central florets are extruding their pollen, the latter is held up by the hairy styles (despite the fact that the ovaries are abortive) which thus form a pollen-laden brush at the centre of the capitulum. It is the habit of the capitula to droop and close at night (or in dull or wet weather, at which time insects' visits are scarce), so that the carpellary ray flowers are forced to touch the extruded pollen masses. When the capitula open again in daylight, the ray florets are extended outwards into their normal day position but the pollen is found to be gathered on the fringe of hairs around the tubular part of the corolla; when the carpellary florets extend so far that they are now directed obliquely downwards the pollen masses glide away from the fringe and slide down the styles until held up by the stigmatic surfaces which have curled to meet the pollen. In wet weather the capitula droop in protection of their pollen but they are usually not closed sufficiently to become pollinated in the above way.

Fruit: when fertilization is complete the capitulum again closes and droops. Meanwhile, the calyx-pappus increases greatly in length and the ovary enlarges. Finally the peduncle becomes erect and the involucre opens to expose a dense mass of feathery achenes, closely resembling the clock-infructescence of the Dandelion, and the achenes are likewise dispersed by wind.

Type 3. **The Daisy** (*Bellis perennis*, L.), fig. 61

Habit: a perennial, with a short, branching underground stem bearing a rosette of leaves; in fields; flowering from March to October.

Inflorescence: a capitulum of ray (ligulate) and disc (tubular) florets on a convex, hollow receptacle, surrounded by an involucre.

Flowers: (*a*) The *Ray Floret*: ligulate, zygomorphic, unisexual (carpellary); epigynous.

Calyx: absent; no pappus.

Corolla: white or tipped with pink; zygomorphic, ligulate or strap-shaped, but, unlike the Dandelion, there is no indication of five teeth; probably all five petals are completely fused. (In the Ox-eye Daisy (*Chrysanthemum Leucanthemum*) the corolla ends in three teeth.) The ligulate part passes at the base into a short tube bearing a few hairs.

Andrœcium: no stamens.

Gynœcium: two carpels, syncarpous, inferior; the corolla is inserted directly on the ovary; the smooth style is furnished with a bilobed stigma. The ovary is unilocular, with a basal ovule.

(*b*) The *Disc Floret*: tubular, actinomorphic, bisexual; epigynous.

Calyx: absent; no pappus.

Corolla: five petals, yellow; actinomorphic, tubular with five teeth above; the corolla is slightly hairy.

Androecium: five stamens, epipetalous; anthers joined (syngenesious).

Gynoecium: two carpels, syncarpous, inferior, inserted immediately below the base of the corolla, as in the ray floret; style with collecting hairs and bifid stigma; ovary unilocular, with basal ovule.

Pollination: the florets are protandrous. Nectar is secreted by a ring of tissue at the base of the style in both ray and disc florets. The mechanism of cross-pollination is the same as that of the Dandelion. The stigmas of the ray florets are receptive before those of the disc florets. Of the yellow disc florets, the outermost are the first to open, shedding their pollen into the anther-tubes, and they are followed, in turn, by the inner florets. By the time the latter are exposing their pollen on the hairy styles (the collecting hairs are absent from the styles of the carpellary ray florets, as they are obviously not necessary in a flower bereft of pollen) the stigmas of the outer florets are receptive; insects alighting at the centre of the capitulum and travelling outward thus pollinate the marginal florets. Cross-pollination may, of course, be effected between florets of different capitula. Self-pollination (of the disc florets) is resorted to in the same way as in the Dandelion.

Fruit: an infructescence of inferior achenes. The achenes of the ray florets are slightly larger and more winged than those of the disc florets. The single-seeded fruits are enclosed within the dry and stiffened bracts of the involucre, which forms a kind of container like that of an open capsule. The small fruits are shaken out of the improvised involucral cup when the plants are swayed by wind.

Fig. 61. *Compositæ. Bellis perennis.*—A, median section of capitulum; outer, white ray florets; inner, yellow disc florets. B carpellary ray floret; note two-lobed stigma and inferior ovary. C disc floret, with tubular, five-toothed corolla; note anther tube and exposed style. D floral diagram of disc floret, $K_0[C_{(5)}A_{(5)}]G_{(\bar{2})}$. E of ray floret, $K_0[C_{(5)}A_{(0)}]G_{(\bar{2})}$.

Centaurea Cyanus.—F median section of capitulum; outer large florets neuter, inner florets fertile. G fertile floret; note pappose calyx; anther tube at top shows pollen brushed out by stylar hairs; bifid closed stigma below; note thick, bulbous and hairy filaments of stamens attached to corolla tube; right, lobes of stigma separating, at second stage of cross-pollination. H floral diagram of fertile flower: floral formula, $K_{\text{pappus}}[C_{(5)}A_{(5)}]G_{(\bar{2})}$; I of neuter flower, $K_0C_{(5)}A_0G_0$.

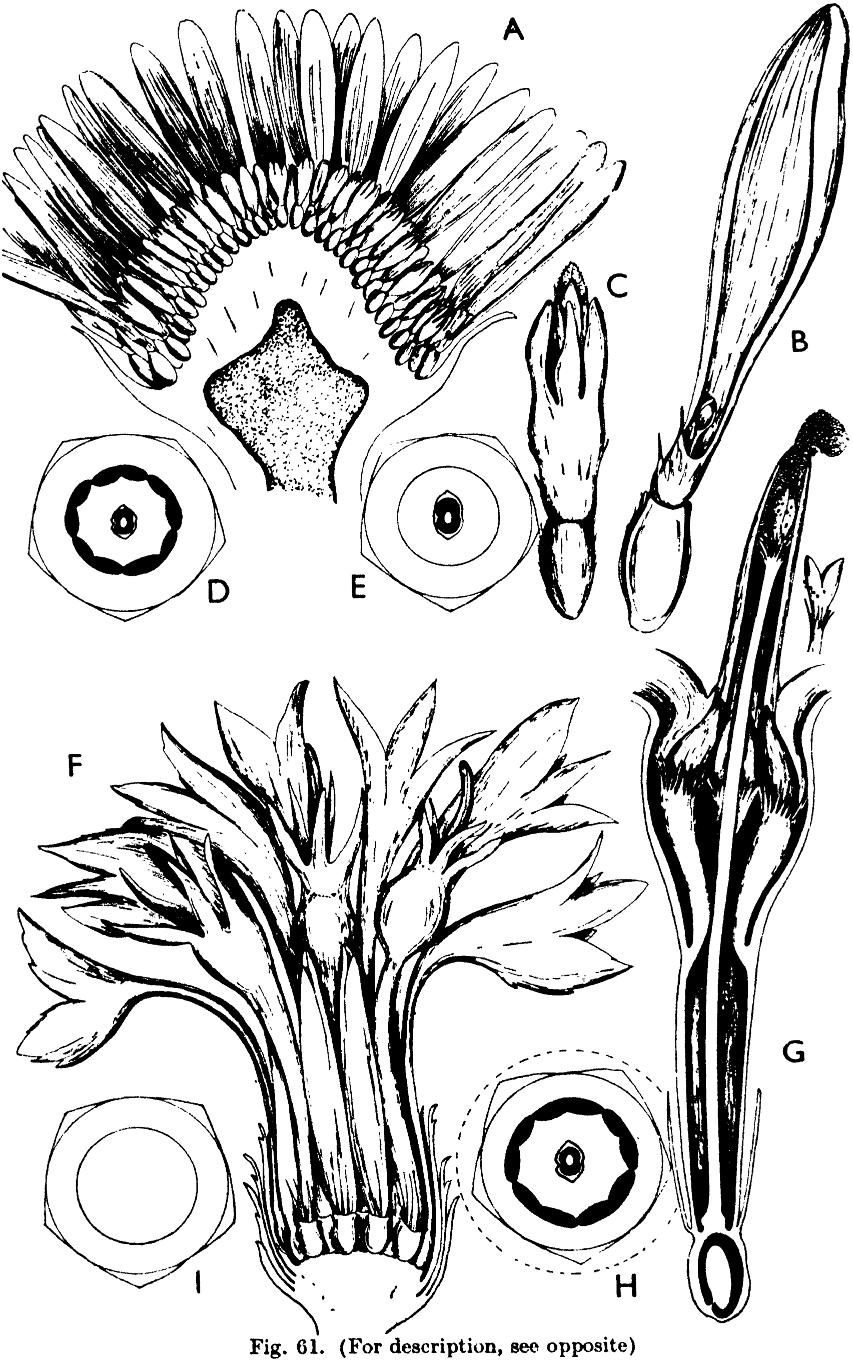

Fig. 61. (For description, see opposite)

Type 4. **The Cornflower** (*Centaurea Cyanus*, L.), fig. 61

Habit: a herbaceous annual of cornfields; also in cultivation. It flowers from June to August.

Inflorescence: a capitulum of neuter, trumpet-shaped, ray florets and narrower, bisexual, tubular disc florets. As compared with the previous types, all the florets are more or less tubular.

Flowers: (*a*) The *Ray Floret*: light-blue; zygomorphic; neuter.

Calyx: absent.

Corolla: zygomorphic; trumpet-shaped, not ligulate as in the previous types. The trumpet is somewhat bilobed but is further dissected into a number of pointed segments furnished with dentate margins. The trumpet stands out at a sharp angle from its narrow, tubular continuation below.

Androecium: no stamens.

Gynœcium: no carpels. The basal part of the corolla tube is slightly dilated, but there is no ovary. These outspread florets serve only to attract insects to the capitulum.

(*b*) The *Disc Floret*: purple; actinomorphic; bisexual; epigynous.

Calyx: represented by a sparse pappus of a firmer and more bristly nature than that of the Dandelion, inserted directly on the edge of the inferior ovary.

Corolla: five blue or bluish-purple petals, sympetalous, tubular below and constricted about half-way up, then becoming bulbous before dividing into five equal, triangular segments. The outermost of these florets are, like the neuter florets, directed obliquely outwards, but the central ones remain more of less erect.

Androecium: five stamens, epipetalous, alternating with the lobes of the corolla; inserted within the corolla-tube at the base of the dilated part. At their points of attachment the five filaments are narrow but they become bulbous above; they are fringed with a circlet of upwardly directed bristles just below the anthers, which unite to form the customary tube; anther dehiscence, as usual, is introrse.

Gynœcium: two carpels, syncarpous, inferior; ovary unilocular, with the usual single and basal ovule. The stout style is of uniform thickness but expands near the apex into an ovoid, bifid stigma. Below the stigma the collecting hairs are more localized than in the previous types, and take the form of a circlet of stiff, upwardly projecting hairs.

Pollination: the fertile florets are strongly protandrous. Nectar is secreted by a small ridge of tissue around the base of the style and collects within the narrow base of the corolla tube. Bees and other insects with a long proboscis are the pollinators. In the first stage of pollination the style elongates and with its circlet of hairs below the stigma acts like a chimney-sweeping brush, forcing out a quantity of pollen which collects at the mouth of the anther tube. Meanwhile, the stigmatic lobes are closed and thus protected against self-pollen though actually surrounded by it. Insects visiting at this stage remove the pollen but in searching in the corolla tube for nectar the proboscis comes into contact with the bulbous filaments of the stamens; such contact stimulates the filaments to contract to such an extent as to draw the anther-tube downwards, a process which results in a further extrusion of pollen. When the insect withdraws from the floret the filaments and anthers return to their first positions; the mechanism is operative several times provided the filaments are stimulated by contact. The second stage in pollination consists in a further elongation of the style so as to carry its termination well above the extruded pollen. Thereafter the bifid stigma opens into its broad thick lobes, which are stigmatic on the inner surface, and insects visiting at this stage effect cross-pollination. The mechanism is not unlike that of the "piston" type, already described in the Lupin (p. 188), but in that flower the corolla, as well as stamens, plays a part, whereas here the mechanism is operated entirely by the stimulation of the staminal filaments. As the stigmatic lobes of the Cornflower are shorter and thicker than those of the Dandelion or Daisy types, it appears that the process of incurling of the lobes (to effect self-pollination by picking up pollen from the collecting brush) is rendered difficult, but selfing, no doubt, may occur at the second stage when the insect comes into contact with the margins of the stigmatic lobes.

Fruit: an infructescence of feathery achenes; dispersed by wind.

MONOCOTYLEDONS

FAMILY 15. CYPERACEÆ (THE SEDGES)

The members of this family, commonly called the Sedges, are herbaceous perennial plants of grass-like habit, but differ from the Grasses in several important features. The linear leaves are furnished with sheaths which are entire, instead of being split along one side; the axis is solid and commonly three-angled, instead of hollow and round as in the Grasses. They occur mostly in marshy places, bogs, moors, pastures, and maritime sandy localities. The Sedges are of little economic importance. The Paper-reed (*Cyperus papyrus*) is a tall riverside plant; thin strips of the stem pressed together formed the ancient writing-paper, papyrus. The Cotton-sedge (*Eriophorum*), erroneously called the Cotton-grass, is a common plant on wet moors; the white tufts of " cotton " consist of perianth-bristles which help in the dispersal of the fruit. By far the largest genus is *Carex*, with about 70 British species growing in diverse situations, chiefly in wet places, pastures, and woods. *Carex arenaria* is the Sand-sedge growing on sand-dunes; its rhizomes help to bind the sand for land reclamation. The inflorescence of the Sedges is compound, the basic unit being a spikelet. The genera *Eriophorum*, *Cyperus*, and *Scirpus* have bisexual flowers; *Carex* has unisexual, rarely bisexual flowers.

Type. The Common Marsh Sedge (*Carex paludosa*, Good.), fig. 62

Habit: a herbaceous perennial with creeping rhizomes and long, stiff leaves; in marshes and on margins of streams; flowering from May to July.

Fig. 62. *Cyperaceæ. Carex paludosa.*—A, plant with staminate spikelets at apex and carpellary spikelets below; lateral spikelet on left is a " mixed " one (see D); note triangular stem and entire leaf-sheaths. B portion of leaf showing leaf-sheath entire (unsplit). C staminate spikelet. D " mixed " spikelet of staminate flowers above and carpellary flowers below constriction. E portion of staminate spikelet with anthers exserted. F staminate flower. G pollen grain, with thick exine and two germ pores. H carpellary spikelet; note exsertion of styles. I portion of carpellary spikelet with stigmas exserted, as in first stage of pollination. J carpellary flower, bract on right; gynœcium (dotted) enclosed in utricle, with 3 divergent styles. K syncarpous gynœcium with style, enclosed in utricle. L nut, within utricle. M floral diagram of staminate flower; 3 stamens in axil of bract. N of carpellary flower; syncarpous unilocular ovary and single ovule, surrounded by two-ribbed utricle, in axil of bract.

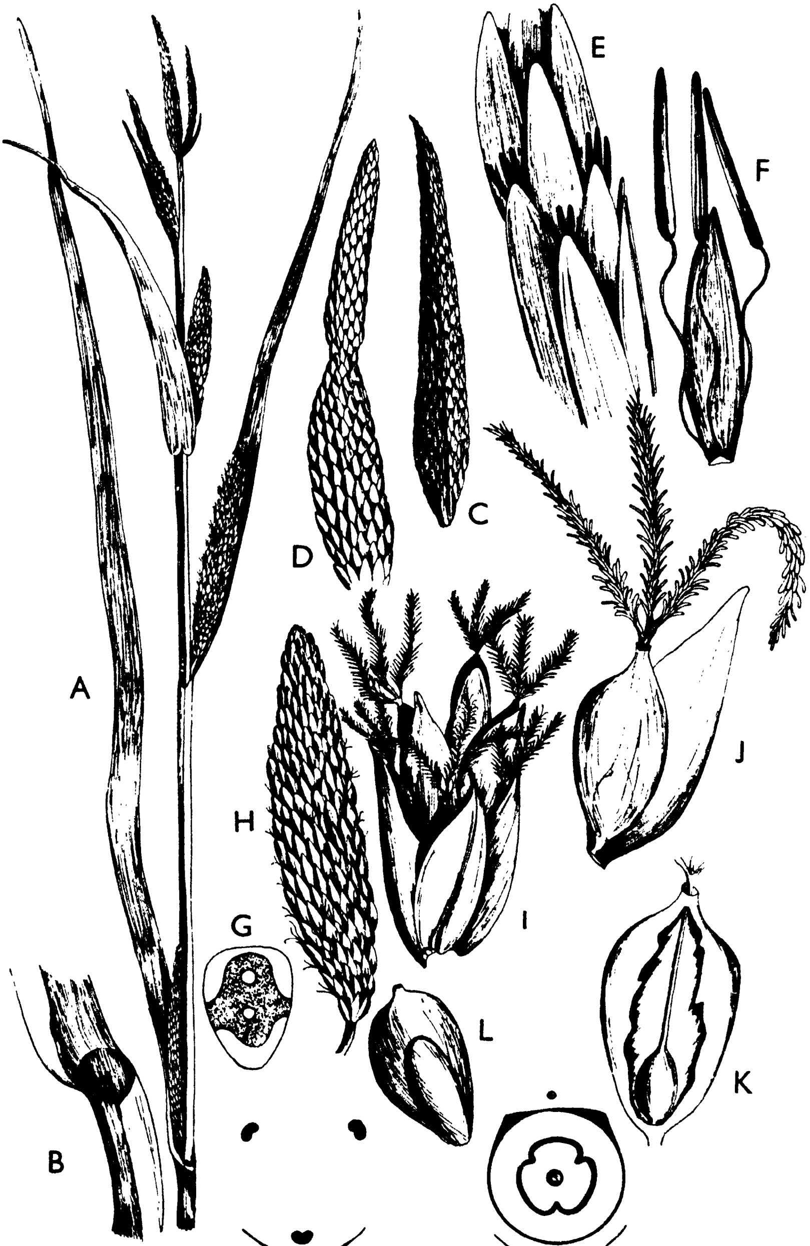

Fig. 62. (For description, see opposite)

Inflorescence: compound, consisting of a number, about six, of sessile (or nearly so) spikelet inflorescences, of which the two uppermost are usually staminate and the remainder carpellary, but the one below the staminate is usually mixed, containing both kinds of flowers (fig. 62, A; third from top).

1. The *Staminate Spikelet*: sessile or sub-terminal in the leaf axil; it is somewhat three-sided, like the three-angled axis, slender and tapering towards the apex. It consists of very numerous small brown bracts which are closely imbricated; the bracts near the base and apex may be found empty, while those towards the middle contain in their axils the staminate flowers.

The *Staminate Flower* is of very simple structure, consisting merely of three stamens with long narrow anthers borne on slender filaments which are capable of considerable extension. Each flower arises in the axil of a bract.

2. The *Carpellary Spikelet*: lateral, on a short stalk in the leaf axil; cylindrical and slightly longer and broader than the staminate spikelet. The imbricating bracts are again very numerous; those near the top and base may be empty, but in the axils of the bracts towards the middle, single carpellary flowers are found.

The *Carpellary Flower*, borne on a very short stalk in the axil of a bract, consists of a bottle-like investment (the *utricle* or *perigynium*, developed from two fused bracteoles). Within it is a superior syncarpous gynœcium of three carpels elevated on a very short stalk; the three-lobed ovary terminates in a long style which passes out at the mouth of the utricle, branching into three divergent stigmas which are covered with long and glandular papillæ. The tri-carpellate gynœcium is unilocular and contains a solitary ovule, in basal placentation.

Bisexual flowers, of three stamens together with the gynœcium as above, are sometimes found in the carpellary spikelets.

3. The *Mixed Spikelet*: usually one on each plant, the third or fourth from the top. The spikelet may be distinguished from the others by being longer and it may also show a definite constriction (fig. 62, D) above and below which are found the staminate and carpellary flowers respectively.

Pollination: the inconspicuous flowers are wind-pollinated; they are protogynous. In the first instance the bracts of the carpellary flowers gape open to allow the extrusion of the branched papillose stigmas. In older plants which have passed through this stage the staminate spikelets exsert their anthers, which hang and sway freely by virtue of their extended filaments, so that the wind-borne, dry pollen is easily caught by the stigmas of the carpellary flowers. In this way cross-pollination between two individuals is effected, for by the time the stamens are extruded in one individual the stigmas of that plant are probably withered.

Fruit: a nut. After fertilization, the stigma and style wither away, and the ripening ovary remains within the utricle. The fruit is rendered buoyant by the swelling of the utricle, which thus assists in its dispersal by wind.

FAMILY 16. GRAMINEÆ (THE GRASSES)

One of the largest families of flowering plants, and the most important from a general economic aspect. They are mostly annual or perennial herbaceous plants, but a few types, e.g. the Bamboo, the West Indian Sugar-cane, the African Reed-grasses, and the Pampas-grasses of South America, grow to great size. Propagation by underground shoots is general, leading to the formation of either a tufted habit if the new shoots are immediately pushed up, or a creeping habit when the new shoots or rhizomes extend horizontally and branch profusely in the soil before appearing at the surface. The rhizomatous habit with its rich system of adventitious roots renders the plants useful as binders of loose soil and shifting sands, especially in the reclamation of marshes and sand-dunes. The sub-aerial stems are usually furnished with prominent solid nodes, and hollow internodes; the narrow, flat leaves are alternate, in two rows, and clasp the smooth, round stem with a close-fitting sheathing base, which (unlike the *Cyperaceæ*) is split all or nearly all the way down on the side of the stem opposite the leaf; at the junction of lamina and sheath there is a thin, papery growth, the ligule, which grows like a collar from the top of the sheath (the shape of the ligule varies considerably in the different genera) and grasps the axis closely. The grasses are a valuable source of food for domestic animals and are constantly being improved upon by selection and plant-breeding. The principal fodder plants, including meadow (hay) and pasture grasses, are Italian Rye-grass (*Lolium italicum*), Perennial Rye-grass (*Lolium perenne*), Cocksfoot (*Dactylis glomerata*), Timothy (*Phleum pratense*), Meadow Fescue (*Festuca elatior*), Tall Fescue (*F. arundinacea*), Red Fescue (*F. rubra*), Sheep's Fescue (*F. ovina*), Meadow Foxtail (*Alopecurus pratensis*), Rough-stalked Meadow Grass (*Poa trivialis*), Crested Dog's-tail (*Cynosurus cristatus*), Yorkshire Fog (*Holcus lanatus*), Sweet Vernal (*Anthoxanthum odoratum*), Tall Oat-grass (*Arrhenatherum elatior*). The valuable cereal grasses include Wheat (*Triticum*), Oat (*Avena*), Barley (*Hordeum*), Maize (*Zea*), Rye (*Secale*), and Rice (*Oryza*). *Saccharum officinarum* is the Sugar-cane. The hollow jointed stems of the Bamboo (*Bambusa, Dendrocalamus*) are elastic and very hard, owing to the deposition of silica; they are extensively used in the manufacture of paper, furniture, mats, baskets, brushes, coarse clothing, rope, weapons, and other implements; the young shoots and seeds are edible.

The Grass inflorescence is usually compound and varies considerably in the different genera. It is built on the spikelet plan. The spikelets may either be arranged on the plant in a loose panicle, e.g. Oat, or they may be sessile on the axis, forming a spike of spikelets, e.g. Wheat, Rye-grass (fig. 63, A). The unit of inflorescence is the spikelet, made up of one or more flowers, not all of which may be fully developed; the flowers are arranged in two rows on a greatly condensed axis (rachis) and the whole spikelet is enclosed within one or two boat-shaped bracts called *glumes*. Further details are given below.

The Grasses are typical anemophilous plants, and are mostly cross-pollinated, but a few (e.g. Wheat) are habitually self-pollinated. The fruit is a caryopsis, a kind of achene in which the pericarp is fused with the testa. The seed is typically endospermous; the monocotyledonous embryo is straight and occupies only a small part of the seed. The endosperm of the cereals forms the valuable floury part of the grain.

Type. **The Perennial Rye-grass** (*Lolium perenne*, L.), fig. 63

Habit: a herbaceous perennial; in pastures and waysides; in flower from June to August.

Inflorescence: compound, indefinite, consisting of a number of sessile spikelets or a spike of spikelets. The spikelets are somewhat compressed and arranged alternately, in two rows, fitting closely edge-wise into the grooved or fluted side of the axis. This protection of one side of the spikelet, within the alternate grooves of the stem, renders unnecessary the presence of a second, inner glume, usual in other types of grasses. (It is, however, present in this type in the terminal spikelet which does not receive the protection of the axis.) On dissection, from the base upwards, a typical spikelet consists of the following parts:

Fig. 63. *Gramineæ. Lolium perenne.*—A, compound inflorescence, a spike of spikelets. B spikelet. C diagrammatic representation of spikelet if its axis (rachis) were capable of extension; note empty, barren glume at right base, and 7 fertile flowers, partially opened. D flower; anterior outer pale (outer flowering glume) pulled down in front, double-keeled, posterior, inner pale (inner flowering glume) stands behind the floral parts, on a brief stalk (rachilla); note ovary surmounted by two feathery stigmas, and flanked at base on each side by scaly lodicules; note large anthers of the three stamens. E median vertical section of ovary and surrounding parts; from right, outer pale; a lodicule; a staminal filament; ovary containing the single ovule attached posteriorly, surmounted by brief style showing parts of stigma (of glandular cells), inner pale; axis. F floral diagram, shown with investing pales and lodicules; floral formula, $P_{2\ \text{lodicules}}A_3G_{\underline{(1)}}$.

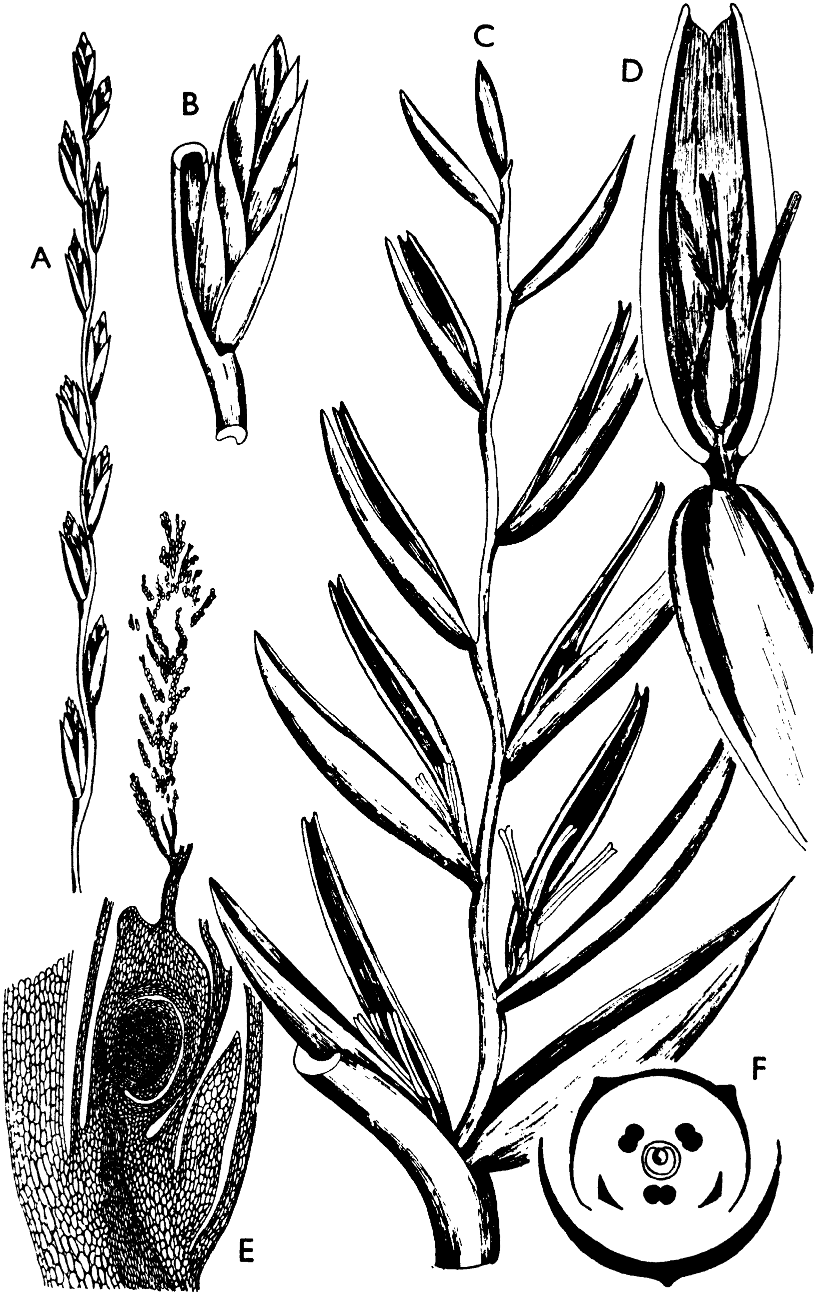

Fig. 63. (For description, see opposite)

(*a*) On the side remote from the axis, and protecting the whole spikelet when in bud, a large, greenish bract called the *barren glume* or *outer glume* (in other types of grasses, there is a second, inner barren glume, on the side facing the axis). The empty glume is inserted directly on the axis.

(*b*) The rest of the spikelet consists of about six to eleven flowers arranged one above the other, alternately on two sides of a greatly condensed axis or *rachis*; one or more of the distal flowers may be ill-developed or aborted. The flowers of a spikelet mature in succession from base to apex.

(*c*) A typical flower, extracted from near the base of the spikelet consists of the following parts:

1. An outer, lower (anterior) bract, the *outer pale* or palea, also called the *outer flowering glume*, inserted directly on the rachis. (In many types, e.g. Oat, Barley, the midrib of the outer pale is prolonged into a stout stiff bristle or *awn*.)

2. An inner, upper (posterior) double-keeled bract (more correctly, perhaps, the equivalent of two fused bracteoles) called the *inner pale*, or inner flowering glume, which is situated on a short stalk, the *rachilla*, in the axil of the outer pale.

3. If the two pales are prised apart (at flowering, they gape open) the floral members are seen to consist of the following:

   (*a*) Two minute membranous scales, called *lodicules*, which stand anteriorly, to the right and left of the superior ovary. They are often regarded as a rudimentary perianth; their function appears to be that of separating the pales at flowering time, when, by swelling, they force these bracts apart.

   (*b*) The *Andrœcium*: three stamens with very long, narrow anther lobes which are divergent at their extremities. The anthers are attached to the filaments at a point behind (versatile); one of the stamens is anterior and the other two lateral. In the young flower the filaments are short, and the three anthers are lodged closely within the inner pale.

   (*c*) The *Gynœcium* consists of a single carpel, superior, on a very brief axis within the base of the inner pale. It contains a single ovule attached by a broad funiculus which merges into the posterior tissues of the ovary wall (fig. 63, E). The small flask-shaped ovary is surmounted by a short style which divides into two feathery and glandular stigmas.

Pollination: the inconspicuous, nectarless flowers of the *Gramineæ* are wind-pollinated. In general, the stamens discharge their pollen at the same time as the stigmas are receptive, but dichogamy may also occur in its protogynous or protandrous form, according to the type. In the generality of Grasses, however, cross-pollination is the rule, because individuals are often sterile to their own pollen. It has been ascertained that a high percentage of sterility exists, e.g. in *Lolium perenne.* The relative productivity of this species obtained by self-pollination and by cross-pollination shows that the latter may give an increase in productivity ranging from 37 to 224 per cent.[1]

At pollination, the parts of the spikelets separate, and as it often happens that the stigmas emerge first, their loose feathery nature is eminently well adapted to catch the dry, powdery pollen conveyed by wind. When the anthers are exserted they are soon pushed clear of their own spikelet by the great extension of the filaments; the large dangling anthers dehisce by wide pores at both extremities and here the pollen collects at the tips of the divergent lobes, as if held in small spoons. The swaying of the anthers in the breeze scatters the pollen in small clouds.

Fruit: a caryopsis, i.e. an achene in which the seed-wall is fused with the pericarp. The yellowish-brown achene is enclosed within the hairy inner pale and the five-ribbed, smooth and awn-less outer pale. The fruit thus compressed between the pales is distinctly boat-shaped and pointed; it comes away enclosed within these two coverings, which by their dry and chaffy nature render the fruit buoyant for wind dispersal.

FAMILY 17. JUNCACEÆ (THE RUSHES)

A small family of herbaceous plants somewhat resembling Sedges and Grasses in general appearance but usually with stiff, cylindrical or flat narrow leaves furnished with prominent sheathing bases. The stems are mostly sympodial rhizomes. These widely spread plants thrive in wet places or at high altitudes. Rushes are commonly employed in basket-, mat-, and chair-making. The plants are usually too coarse to serve as fodder for animals. The inflorescence is compound, consisting of compact cymes. The floral structure is close to that of the next family, the *Liliaceæ*, but differs markedly in the inconspicuous dry, bracteate character of the perianth, and in anemophily. The principal genera are *Juncus* and *Luzula.*

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[1] "Self- and Cross-fertilization in *L. perenne*," T. J. Jenkin (*Journal of Genetics*, Vol. XVII, 1926).

Type. **The Field Woodrush** (*Luzula campestris*, DC.), fig. 64

Habit: a herbaceous perennial; common in dry pastures, woods, lawns, &c.; flowering from April to June.

Inflorescence: a panicle of about three to six cymose clusters, usually on slender peduncles, but often with one sessile cluster, arising in the axil of the sheathed leaf. A cyme (fig. 64, B) consists of a basal pair of brown bracts subtending about six or more sessile flowers, one above the other around a short axis; each flower is again enclosed within a pair of bracts.

Flower: actinomorphic; bisexual; hypogynous.

Perianth: six bract-like segments, brown with yellowish margins, free, pointed; in two whorls of three members each.

Andrœcium: six stamens, in two whorls of three, alternating with the members of the perianth. Each stamen is attached to the base of a perianth segment (epiphyllous) by a short filament and bears a long tapering anther which dehisces introrsely; the pollen grains usually remain adherent in tetrads.

Gynœcium: three carpels, syncarpous, superior; unilocular; the broadly ovoid ovary is surmounted by a short style which branches into three elongated stigmas which are not so " feathery " as those of the Sedges and Grasses. There are three basal ovules, one subtending each carpel (fig. 64, G).

Pollination: the flowers are strongly protogynous. The perianth opens just sufficiently to allow the stigmas to emerge; this first stage can often be detected from the general greyish appearance of the plants due to the extruded stigmas. Later, when the perianth segments are expanded to their fullest extent, the stigmas are in a withered condition, and it is only after several days that the plants display their outspread yellow anthers. This second stage of pollination is usually evident from the yellowish hue given to the plants by the exposed anthers. The dry pollen is set free in small clouds and carried by wind to the exposed stigmas. The interval of time between the maturity of the numerous flowers, together with the long period of flowering, renders cross-pollination likely.

Fruit: a capsule, opening into three valves along the dorsal sutures. The seeds are endospermous and are dispersed by hygroscopic action of the dry valves.

Fig. 64. *Juncaceæ. Luzula campestris.*—A, panicle of three cymose clusters of flowers. B cymose inflorescence of 7 flowers with exserted stigmas. C young flower in protogynous condition showing exserted stigmas. D older pollinated flower with withered stigmas. E flower of stage shown in C, opened out to show stamens closely protected by perianth. F gynœcium; note 3-lobed, tricarpellate ovary with 3 free styles. G unilocular ovary in vertical section showing 2 of the 3 basal ovules. H floral diagram; floral formula, $[P_{3+3}A_{3+3}]G_{(3)}$.

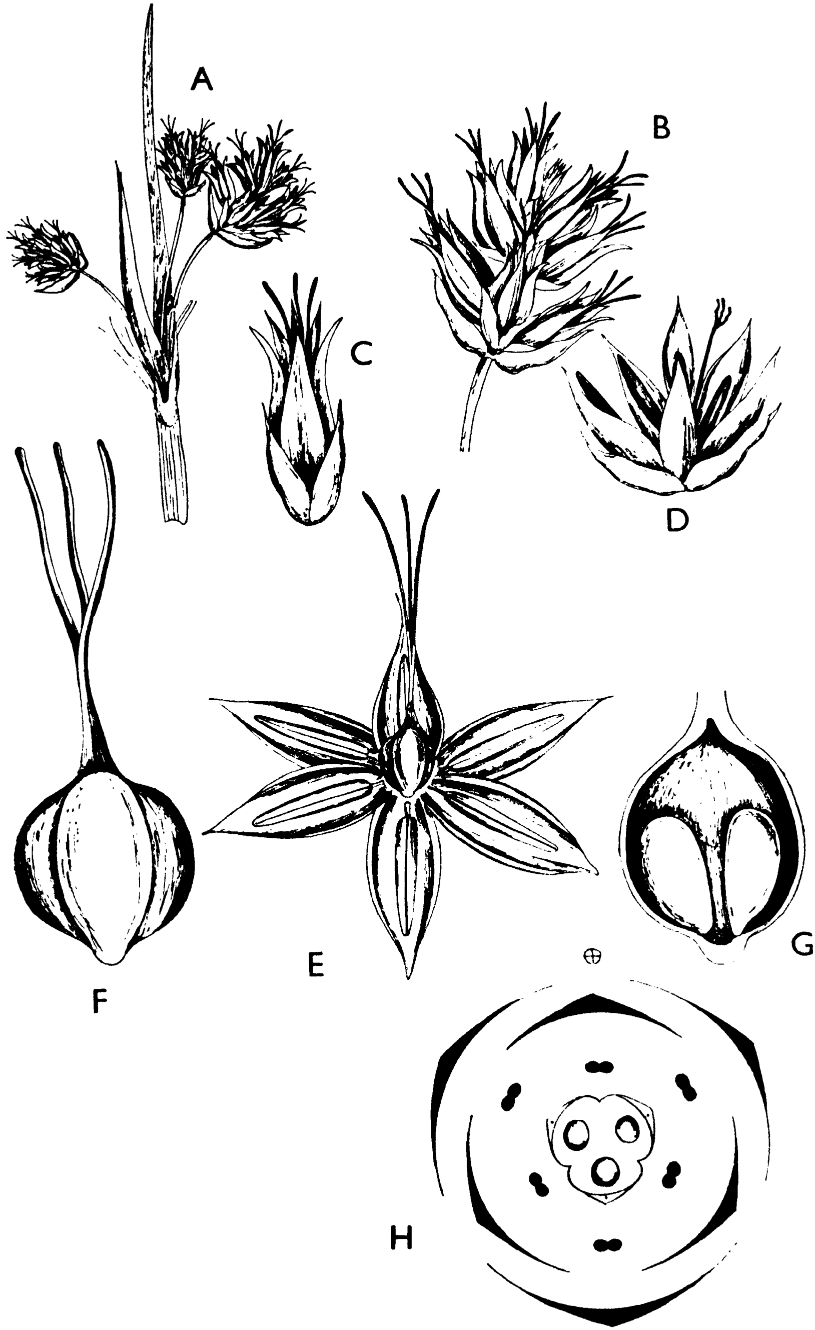

Fig. 64. (For description, see opposite)

FAMILY 18. LILIACEÆ

One of the largest families of flowering plants and the most typical of the Monocotyledons. They are chiefly herbaceous perennials propagating by bulbs or rhizomes; some tropical types are trees or shrubs, e.g. *Dracæna* (Dragon's-blood), so called from the resin exuded by the bark; *Yucca* (Adam's-needle), a common type in cultivation, with enormous inflorescences (pollinated by a moth which lays its eggs in the ovary of the flower and thereafter conveys pollen to the stigma); *Aloe*, which yields the drug aloes. The family is noted for the various kinds of climbing devices and flattened leaf-like stems (phylloclades), e.g. *Smilax*, with axillary tendrils and recurved hooks on the stems; *Asparagus*, with leaves reduced to scales; *Ruscus*, the shrubby Butcher's-broom, with phylloclades; *Gloriosa*, with leaf-tip tendrils; *Semele*, a climber with phylloclades. The family has a large number of garden or ornamental plants: Lilies of numerous species, Scilla, Hyacinth, Muscari, Fritillary, Gagea, Kniphofia, Agapanthus, Tulip &c. British plants include Herb Paris, Solomon-seal, Lily-of-the-Valley, Lloydia (only on the Snowdonian Range), Star-of-Bethlehem, Wild Hyacinth (English Bluebell), Garlic, Bog Asphodel, and Meadow-Saffron. A few plants are of economic value, e.g. Onion, Chives, Shallot, Leek, Garlic (all different species of the genus *Allium*) and Asparagus. Fibre is obtained from *Phormium*, the New Zealand Flax, and also from *Yucca*; *Aloe*, *Colchicum*, *Veratrum*, *Smilax* (Sarsaparilla), *Urginea* (Squill) yield drugs. The inflorescence is usually a raceme and the floral structure in general is very uniform.

Type 1. **The Tulip** (*Tulipa*, of any cultivated variety: *T. sylvestris*, L., is indigenous in E. and S.E. England), fig. 65

Habit: a herbaceous perennial with a bulbous stem; in meadows and cultivation; flowering in April and May.

Infloresence: solitary.

Flower: actinomorphic; bisexual; hypogynous.

Perianth: six segments, free, yellow (or variously coloured); in two whorls of three, in alternation. Before flowering, the outer segments are green, assist in photosynthesis, and protect the parts within

Fig. 65. *Liliaceæ. Tulipa.*—A, median longitudinal section of flower (anther of posterior stamen on left omitted to show overlapping of perianth segments). B front and side views of dehiscent anther. C three-lobed stigma, from above; note papillose stigmatic ridges. D side view of a papillose ridge (magnified) with pollen grains. E transverse section of triangular, trilocular ovary showing axile placentation. F floral diagram; floral formula, $P_{3+3}A_{3+3}G_{(3)}$.

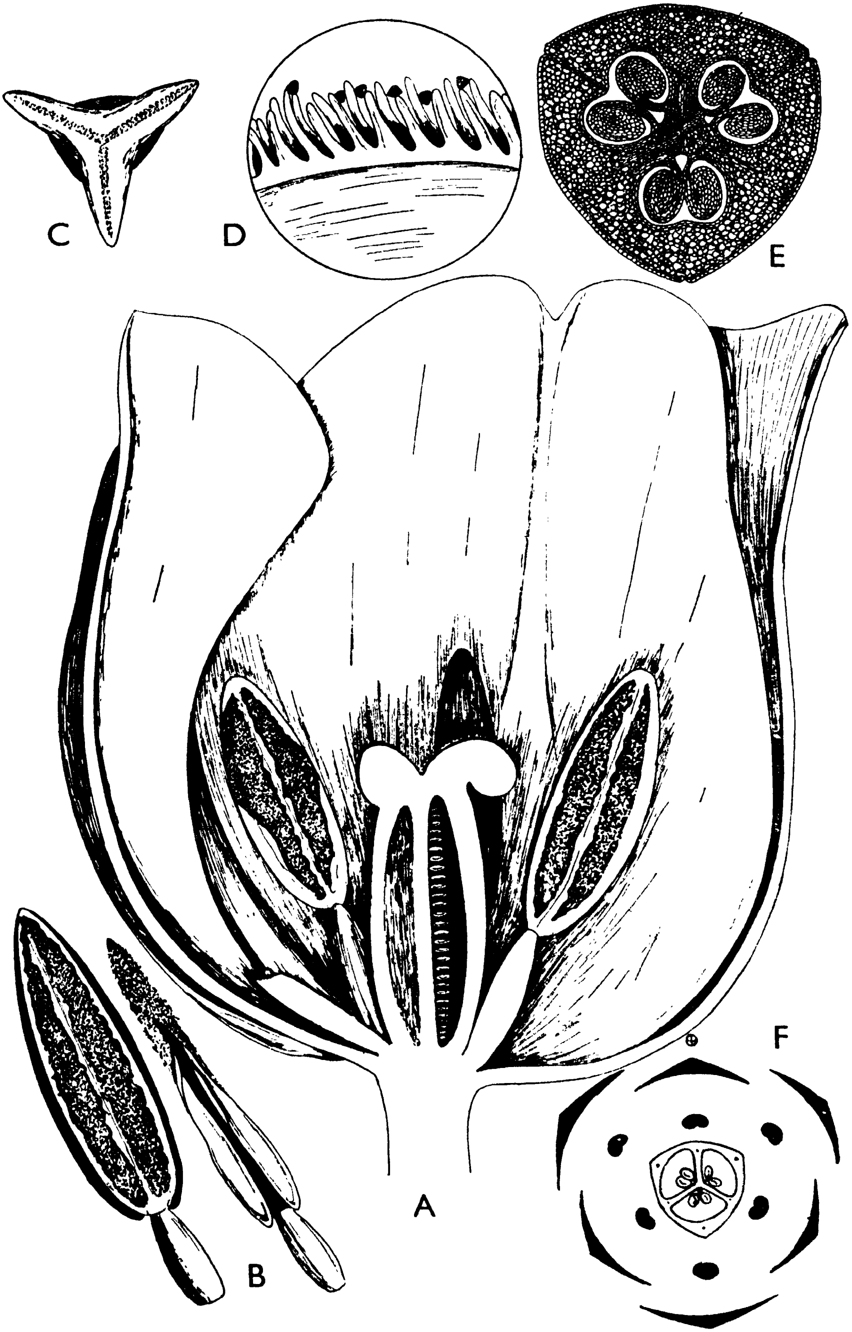

Fig. 65. (For description, see opposite)

but become brightly coloured as the flower matures. The segments of the two whorls overlap.

Androecium: six, in two alternating whorls, free, inserted very close below the base of the ovary. The long arrow-shaped anthers are longer than the filaments; the anthers are delicately pivoted at the tips of their pointed filaments, to which they are somewhat loosely attached, so that they are capable of a certain amount of rotatory movement. Dehiscence is introrse.

Gynoecium: three carpels, syncarpous, superior; the elongated, three-angled ovary is destitute of a style and the apex is expanded into three radiating lobes which are stigmatic along their median crests. The stigmatic papillæ are long and glandular and directed obliquely towards the exterior of the flower (fig. 65, C, D). The ovary is trilocular with numerous ovules in axile placentation.

Pollination: both wild and cultivated Tulips are often infertile. Nuclear abnormalities are known to occur in the pollen and ovules. In the former meiosis is irregular, while the divisions in the embryo-sac frequently result in the formation of diploid nuclei. A large number of species and forms are of triploid nuclear constitution and highly sterile. The species must therefore depend very largely on bulb culture for its continued existence.

Fruit: rarely formed; a capsule.

Type 2. The Wild Hyacinth (*Scilla nutans*, Sm.), fig. 66

Habit: a bulbous perennial; in woods; flowering from April to June.

Inflorescence: a simple raceme; each flower arises in the axil of a bluish-coloured bract and bears on its stalk, towards the posterior side, a shorter and narrower bracteole or prophyll.

Flower: actinomorphic; bisexual; hypogynous.

Perianth: of six blue segments, slightly united at the base (gamophyllous); in two whorls of three, alternating and closely overlapping, giving the flower a tubular appearance; the segments diverge at the top and end in narrow curved tips.

Androecium: six stamens, in two whorls of three, attached to the base of the perianth segments; those of the outer whorl are slightly taller than those of the inner; the arrow-shaped anthers are attached to rather stout filaments; dehiscence is introrse.

Gynoecium: three carpels, syncarpous, superior. The three-lobed

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Fig. 66. *Liliaceæ. Scilla nutans.*—A, flower in axil of bract (left) and with prophyll (right) on pedicel. B median section. C capsular fruit, showing dehiscence at dorsal sutures. D floral diagram; floral formula $[P_{(3+3)}A_{3+3}]G_{(3)}$.

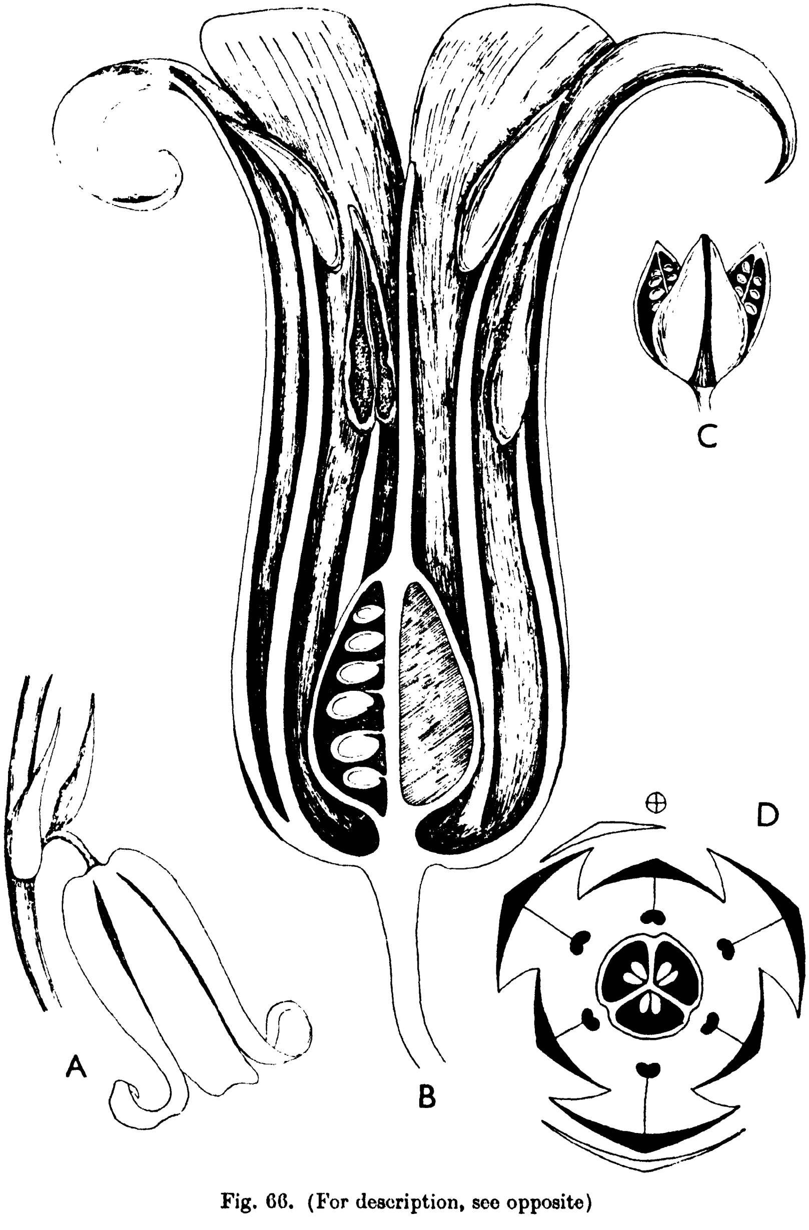

Fig. 66. (For description, see opposite)

pear-shaped ovary terminates in a single style with a three-lobed stigma. The ovary is trilocular with axile placentation.

Pollination: the pendulous flowers (the pollen is thus protected from rain) are rendered attractive to bees by their scent and nectar which is exuded from tiny pockets at the top of the ovary just above the partitions (septal glands). The drooping attitude is assumed only at maturity. The insect alights at the orifice of the bell-shaped perianth and may possibly effect cross-pollination. There is no clear evidence of any interval of time between the maturity of stamens and stigmas (dichogamy), and self-pollination is, no doubt, widespread on account of the close proximity of the stigmas to the introrse anthers, particularly of the taller stamens. The plants propagate extensively by their deeply-planted bulbs.

Fruit: a capsule opening into three valves along the dorsal sutures. The valves become dry and crinkly; the black seeds are liberated into the base of the valves, whence they are shaken out when the plants are agitated by wind.

FAMILY 19. AMARYLLIDACEÆ

A family of tropical or sub-tropical, chiefly herbaceous perennial plants, living in dry climates and mostly of xerophytic habit; they perennate by bulbs and rhizomes. Many types are common plants of cultivation, e.g. the Daffodil (*Narcissus Pseudo-Narcissus*), Pheasant's-eye (*Narcissus poeticus*), Jonquil (*Narcissus Jonquilla*), all of which show a trumpet-shaped addition ("corona") to the perianth; the Snowdrop (*Galanthus nivalis*); Snowflake (*Leucojum vernum*); the Cape-tulip (*Hæmanthus*); the Century-plant (*Agave*), long-lived, with a rosette of large fleshy leaves rich in food-reserve, and coated with thick wax; this plant yields useful fibre (sisal hemp). *Alstrœmeria*, *Amaryllis*, and *Bomarea* are commonly cultivated. In floral structure the family is very close to the *Liliaceæ*, from which it differs in the ovary being inferior. The inflorescence is cymose and usually enclosed within a pair of fused bracteoles called a *spathe*. Floral structure is very uniform and the Narcissi species conform, in general, to the following type.

Type. **The Jonquil** (*Narcissus Jonquilla*, L.), fig. 67

Habit: a herbaceous perennial; cultivated; flowering in April and May.

Fig. 67. *Amaryllidaceæ. Narcissus Jonquilla.*—A, median section of flower. B flower from above (cf. F). C longitudinal section of portion of corolla tube, showing lower anthers in position. D 3-lobed stigmatic crater. E transverse section of triangular ovary with axile placentation. F floral diagram; floral formula, $[P_{(3+3+\text{corona})}A_{3+3}]G_{(\bar{3})}$.

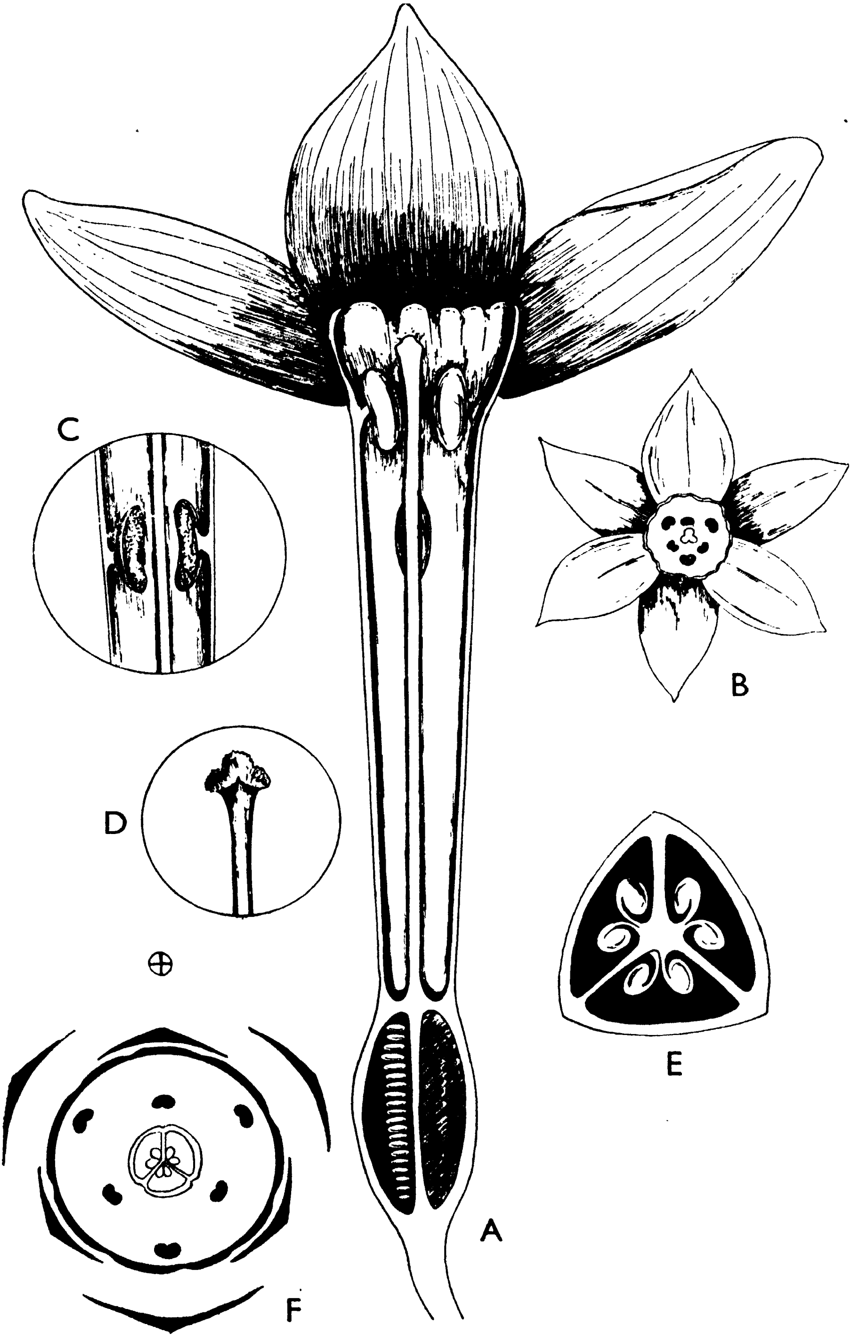

Fig. 67. (For description, see opposite)

Inflorescence: cymose; arranged closely so as to resemble an umbel; flowers protected by a bracteate spathe.

Flower: actinomorphic; bisexual; epigynous.

Perianth: of six cream-white lobes, spreading but joined (gamophyllous) at the base to form a deep and narrow tubular perianth. Within the bases of the six outspreading segments and appearing as if it were a continuation of the perianth tube below, is a collar or trumpet-shaped growth known as the "corona". (The exact morphological nature of the corona is uncertain, but it is the last part of the perianth to develop; there are various interpretations, e.g. that it is an outgrowth of the bases of the perianth lobes; or the combined ligules (cf. *Caryophyllaceæ*) of the six perianth lobes.)

Andrœcium: six stamens, epiphyllous; the outer whorl of three, opposite the outer perianth segments, is situated at the base of the corona; the inner whorl of three is lower down and well inside the corolla tube, and these stamens face the inner perianth segments. All six stamens are furnished with short filaments. The anthers are elongated and kidney-shaped; dehiscence is introrse.

Gynœcium: three carpels, syncarpous, inferior. The cylindrical ovary is slightly wider than the corolla tube within which the long style is carried up to the level of the corona and well above the uppermost stamens. The style ends in a three-lipped stigmatic expansion which is slightly concave within. The ovary is trilocular, with the ovules in axile placentation.

Pollination: the flower is protogynous and pollinated by moths. Nectar is secreted by three deep-seated pockets at the apex of the ovary (septal glands) and collects within the base of the corolla tube. The deeply-placed nectar can be reached only by insects with a long proboscis. The narrow orifice of the perianth-tube compels the moth to touch the expanded crater-like stigma first, and thus cross-pollination may be effected; in its withdrawal from the flower the moth picks up pollen from the two sets of stamens, and the outspreading lips of the crater-stigma may prevent the deposit of self-pollen.

Fruit: a capsule.

FAMILY 20. IRIDACEÆ

A small family of tropical or dry temperate regions; mostly herbaceous perennials propagated by corms, rhizomes, or tubers. The common wild or cultivated types include the Yellow-flag (*Iris Pseudacorus*), the Gladdon or Stinking-Iris (*I. fœtidissima*), the Golden Crocus (*Crocus vernus*), *Gladiolus*, *Ixia*, *Freesia*, and *Tritonia*. *Iris florentina* yields Orris-root, used in perfumery.

Type. The Yellow Flag (*Iris Pseudacorus*, L.), fig. 68

Habit: a herbaceous perennial with a sympodial rhizome bearing stiff, sword-shaped leaves; in marshes and on banks of streams; flowering from May to August.

Inflorescence: cymose; the oldest flower terminates the axis and usually one or two flowers in bud may be found concealed by the bracteate spathe; the whole system is built on sympodial or monochasial lines.

Flower: actinomorphic; bisexual; epigynous.

Perianth: six yellow segments, free above but joined below to form a tube; the segments of the perianth are in two whorls of three members each, the whorls differing greatly in size and form. The free parts of the outer whorl with broad, drooping lobes, spotted with orange and bearing " honey-guides " on their inner surface, form the most conspicuous members of the flower. The three members of the inner whorl are small, arrow-shaped segments and stand erect with incurved tips; they alternate with the outer segments. (The other prominent members, coloured like the perianth, are the stylar parts of the gynœcium and are described below.)

Andrœcium: one whorl of three stamens (if the flower is compared with the typical liliaceous form, an inner whorl of three stamens must be regarded as suppressed). The stamens are inserted at the base of the three outer perianth lobes where the latter unite to form the perianth-tube. Their broad filaments are curved to the shape of the crested petaloid styles with which they are in close contact; the long anthers shed their pollen towards the exterior (extrorse), that is, directly facing the outer segments of the perianth; each stamen, therefore, is protected above by one of the over-arching petaloid styles and below by one of the segments of the outer perianth. The stamens are thus almost entirely concealed from outside view. In spite of the omission of a possible inner whorl of three stamens the mechanism of pollination is a highly effective one.

Gynœcium: three carpels, syncarpous, inferior, surmounted by a short style which divides into three broad stylar arms resembling parts of the coloured perianth (petaloid). The arms are convex above (over-arching the stamens), and stand directly over and in close contact with the three large members of the outer perianth. The tip of each stylar arm broadens out into two convex lobes which stand erect in the flower, like petaloid crests; a crested stylar arm, with a perianth lobe immediately below it, thus forms a two-lipped structure. Across the outer base of each bilobed crest, just where it touches the perianth lobe below, is a narrow, curved, projecting ridge of a thin papery texture; the *upper surface* of the ridge is stigmatic. The three petaloid stylar arms with their prominent crests assist the perianth in making the flower attractive, for the actual stigmatic parts are greatly reduced and consist merely of the three papery ridges. The ovary is trilocular and the numerous ovules are arranged in axile placentation; the loculi stand exactly in line with the three stylar arms.

Pollination: the flowers are visited by humble-bees and hover-flies. To observe the nectaries, one of the lobes of the drooping perianth should be pulled well down, and at the hinge between its base and that of the tubular perianth there will be found on each side a pair of small protuberances, which are the nectaries (fig. 68, D and F). The secreted nectar may collect either here, at the hinge, where it is accessible to bees, which have a short proboscis, or it may flow into the deeper perianth-tube below, where it is out of reach of bees but not of hover-flies, which have a longer proboscis. It is clear that the insect can visit only a third of the flower at a time. Alighting on one of the prominent lobes of the drooping perianth, also rendered attractive by its orange-spotted surface and the directive " honey-guides ", the insect depresses the lobe, and as it thrusts its body below the stylar crest, its head immediately comes into contact with the *upper surface* of the projecting papery stigmatic ridge; if the insect is already covered with pollen from another flower, cross-pollination is thus effected. In further probing for nectar, the insect's head and back come into contact with the outwardly exposed pollen from the anther, but there is no possibility of this pollen being deposited on the stigmatic ridge when the insect withdraws from the flower, because the insect automatically lifts the ridge from below and the lower surface is not receptive. It is possible that a single visit to a flower, that is, to only one-third of it, is effective in cross-fertilizing all of the ovules, despite their occurrence in three separate loculi of the ovary, for the three stylar arms are joined together by a common style down which all the pollen tubes must pass before reaching the ovules. If this is not the case, and the insect passes from one part to another of the same flower, then self-pollination takes place, as the pollen comes from separate anthers of the same flower. It is known, however, that several varieties of the genus *Iris* (cf. Tulip) are triploid with a high degree of sterility; such forms may

Fig. 68. *Iridaceæ. Iris Pseudacorus.*—A, flower, with another in bud, in axil of spathe B flower from below; note inferior ovary and perianth segments. C median vertical section; note anther with extrorse dehiscence. D outer perianth lobe pulled down to show stamen attached to its base, and crested stylar arm behind. E stigmatic ridge or flaps at base of crest. F basal part of perianth lobe with base of stamen in middle, and a pair of nectaries on each side; the dark-shaded parts lead down into the tubular perianth. G perianth lobes cut away from tubular part to show the three stylar arms and crests. H transverse section of trilocular ovary, showing axile placentation. I capsular fruit. J same, open along dorsal sutures. K floral diagram; floral formula, $[P_{(3+3)}A_{3+0}]G_{(\bar{3})}$.

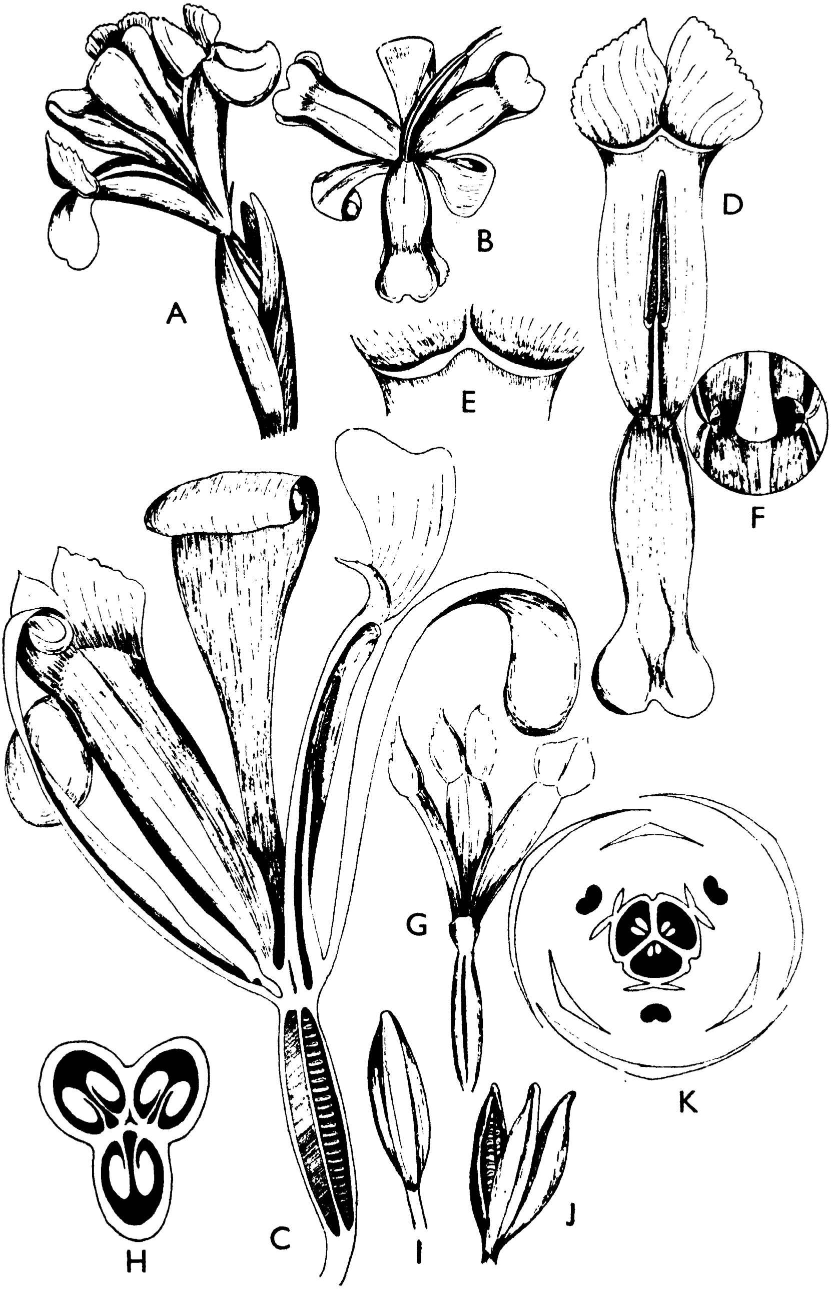

Fig. 68. (For description, see opposite)

depend entirely on vegetative means (by division of the rhizome stem) for their continuance. It is probable that fruits are formed only as the result of cross-pollinations between distinct flowers.

Fruit: a capsule, opening along its three dorsal sutures; each valve is accordingly furnished with one of the three axial partitions, on each side of which are numerous flat seeds. The latter are easily dislodged from the valves and are sufficiently thin to be carried away by the wind.

FAMILY 21. ORCHIDACEÆ

A large family of perennial herbaceous plants mostly tropical, exhibiting a wide range of structure according to habitat. Many tropical epiphytic types grow on trees; the small seeds germinate in the crevices of the bark and when a rooting system has been formed, organic matter is caught in the tangle of roots, into which more branch-roots penetrate; other roots hanging freely in the air are covered with a water-absorbing tissue called velamen. A few types are entirely saprophytic and bereft of green leaves; the Bird's-nest Orchid (*Neottia*) has an underground stem with a dense mass of roots immersed in humus; the roots are invested by a fungal mass called mycorhiza which assists in feeding the plant. The Coral-root Orchid (*Corallorhiza*) is of similar habit but has no roots, the underground stem being furnished with absorptive hairs. The average types of temperate climes are terrestrial plants, the underground parts of which usually possess a tuberous system consisting partly of root and partly of stem. In some forms the mycorhiza is internal, in others external to the host plant.

The family is noted for its great array of brilliantly coloured flowers, many of which are rare and difficult to cultivate. In diversity of floral structure and elaborate methods for ensuring cross-pollination this family is perhaps the most highly specialized of all the flowering plants. The flowers of some exotic types assume grotesque shapes, and it is these forms which display the more interesting mechanisms for pollination. Curiously, however, very few secrete free nectar, and the visiting insects usually puncture the succulent tissues of the perianth (e.g. the spur) for the sweet juice they contain. Of great interest are the

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Fig. 69. *Orchidaceæ. Orchis maculata*—A, young spike inflorescence in vertical section (the section is not truly median; the flower shown here at the top is lateral on the axis); note orientation of young flowers in relation to bract and axis; the spurred labellum faces the axis and is therefore posterior. B spur, facing axis (on right); overhanging entrance to spur is the rostellum, within which may be seen the disc of a pollinium; the glandular tissue on left below rostellum is a stigmatic area; below, part of ovary showing lobed placenta. C apical part of young pollinium, in longitudinal section, showing central columella surrounded by massulæ consisting of pollen-grains (in bi-nucleate condition). D ovary, in longitudinal section, showing greatly lobed parietal placentæ, as yet without ovules.

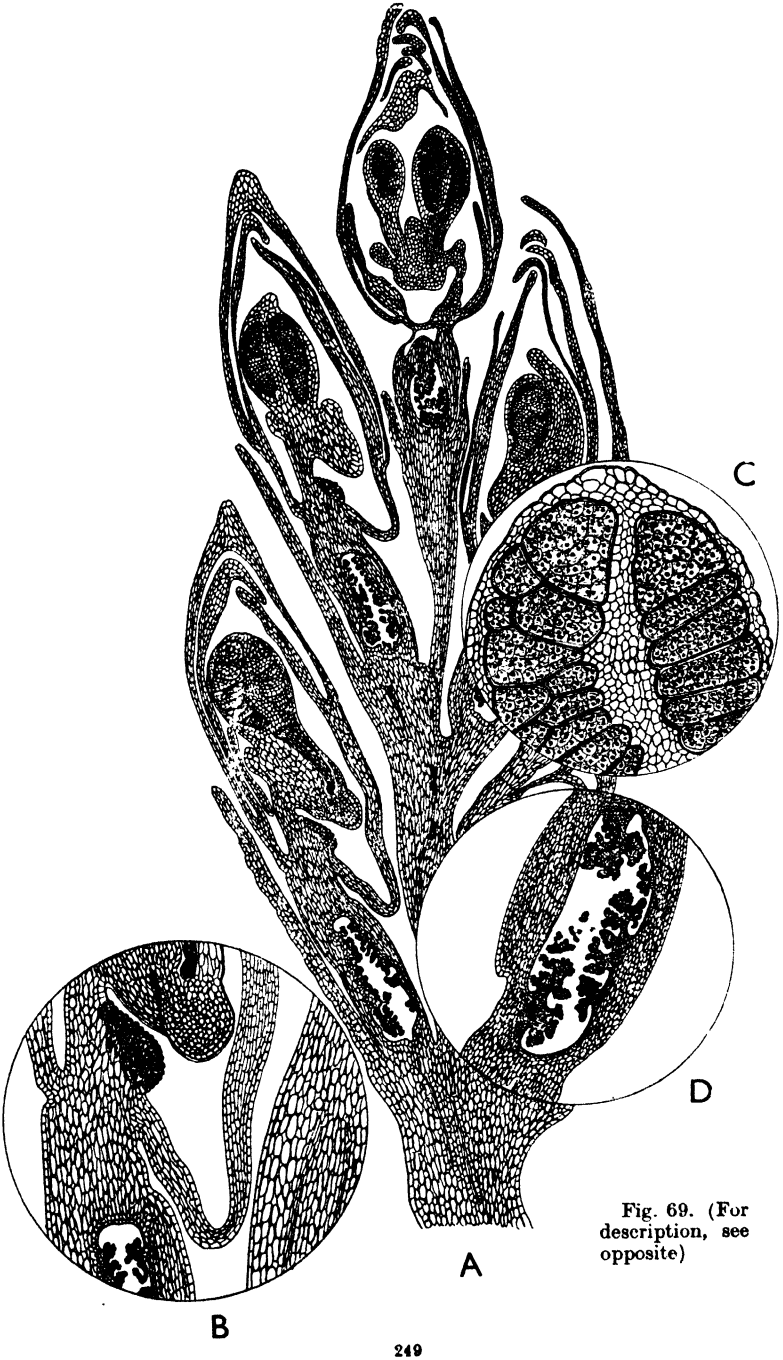

Fig. 69. (For description, see opposite)

structure of the anther and the peculiarity that the pollen is massed into adhesive packets called *massulæ* which are again aggregated into club-shaped bodies known as *pollinia*; an anther usually has two such pollinia. The latter are partly inserted within a gummy cup or *rostellum*, which the insect ruptures when visiting the flower; as the insect withdraws, the pollinia are removed and remain adherent to its head. The adaptations for the transference of pollinia to the visiting insect are of a very varied nature and are fully described in Darwin's *Fertilization of Orchids*. Among the more interesting types are *Coryanthes* and *Stanhopea*, which are epiphytic forms of tropical America; these possess showy pendulous flowers which entrap the visiting insect, and as there is only one way of exit, the insect is forced to touch first the stigma, and then the pollen. Part of the perianth of *Cattleya* and *Epipactis* is so sensitive to contact that the insect is propelled against the gummy rostellum, which then ejects adhesive fluid over the insect, thereby cementing the pollinia to its body before it leaves the flower. The pollinia of *Mormodes* and *Catasetum* are violently shot out when the visiting insect touches the *column* (see below). Cultivated greenhouse types include *Cattleya*, *Dendrobium*, *Eria*, *Vanda*, *Cypripedium* (Lady's-slipper), *Oncidium* and *Cymbidium*. The British types include several species of the genus *Orchis*, namely, Green-winged Orchis (*O. morio*), Soldier Orchis (*O. militaris*), Early-purple Orchis (*O. mascula*), Spotted Orchis (*O. maculata*). Other types are Butterfly Orchis (*Habenaria bifolia*), Frog Orchis (*H. viridis*), Bee Orchis (*Ophrys apifera*), Fly Orchis (*Ophrys muscifera*), Tway-blade (*Listera ovata*) and Lady's-tresses (*Spiranthes*). The family is of little economic importance; the pods of *Vanilla planifolia* yield the flavouring substance vanilla.

Type. **The Spotted Orchis** (*Orchis maculata*, L.), figs. 69-71

Habit: a perennial herb with underground tubers which contribute to both shoot and root development; the leaves are usually spotted; in pastures, meadows, and woods; flowering from June to September.

Inflorescence: a spike; the flowers arise in the axils of strongly-veined bracts; the twisted " stalks " are not merely pedicels but the elongated inferior ovaries, which during development twist through a half-circle.

Fig. 70. *Orchidaceæ. Orchis maculata.*—A, flower, front view; labellum cut away but spur left intact; other perianth lobes are also removed to show anther with its two pollinia attached to shield or column behind; note the two staminode protuberances to right and left of the shield; rostellum at centre, above entrance to spur, with the two sunken stigmatic areas to right and left; twisted ovary below. B pollinium; massulæ, caudicle, and disc. C pollinium dissected to show adherent massulæ. D massula and its pollen. E germinating massula, in water. F twisted ovary cut across to show the three parietal placentæ; bract behind.

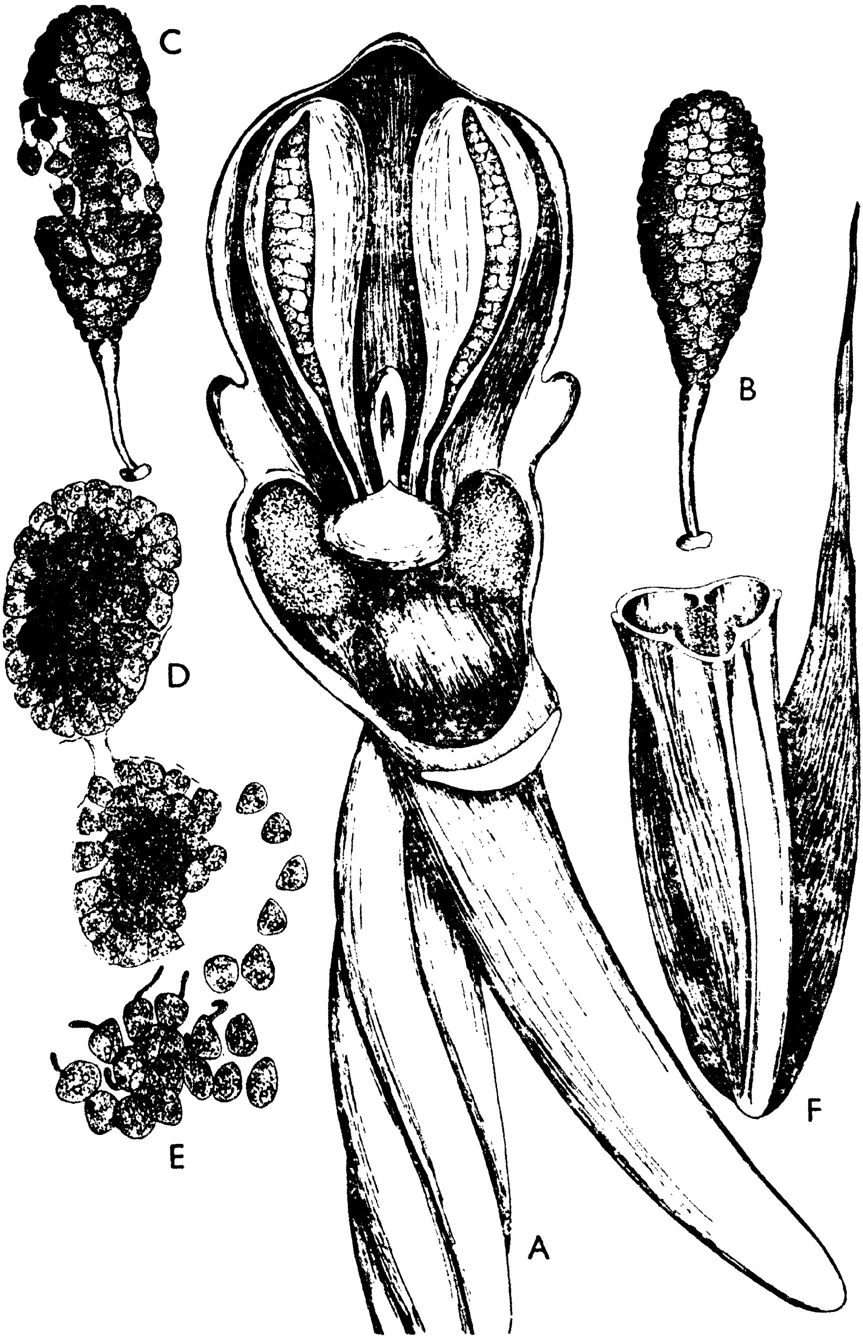

Fig. 70. (For description, see opposite)

Flower: strongly zygomorphic; bisexual; epigynous.

Perianth: variable in colour, pinkish-white or purple; of two whorls of three members each, very slightly united at the base and attached to the top of the ovary. The segments of the outer whorl are narrow, as are also two of the inner whorl, all of which remain more or less erect and overlapping in protection of the inner members of the flower; the third segment of the inner perianth forms a broad lip, the *labellum*, which is prolonged behind the flower into a hollow spur almost as long the ovary. There is no nectary, but the visiting insect punctures the succulent tissue of the spur for the sweet juice it contains.

Andrœcium: one stamen. If all the perianth lobes are removed and the labellum cut away except for the spur (see fig. 70, A), the two lobes of the anther will be seen side by side and fused behind to a shield-shaped structure called the *column*; the latter is probably the equivalent of an expanded connective. Again, a side view of the shield, as seen in a median longitudinal section (see fig. 71), shows it to be a solid prolongation of the tissue above the ovary; in other words, the anther of the single stamen is fastened by means of its enlarged connective (the column) to the top of the ovary. If we look again into the front of the flower, we see that each lobe of the anther is covered by a thin membrane which splits open from apex to base, exposing a club-shaped body, the *pollinium*. The latter is easily extracted (see " pollination " below). It consists of three portions, a club-shaped *head* carried on a stalk or *caudicle* which expands at the base into a small sticky *disc*. Dissection of a pollinium shows that the caudicle is continued into the head as a supporting tissue or columella, around which are massed together packets of pollen, or *massulæ* (fig. 70, C, D). The latter are not of uniform size and shape, but are separated from one another by thin membranes. Each massula, in turn, consists of a large number of irregularly shaped pollen grains (usually in a bi-nucleate condition) densely packed together, so that a young massula appears to be of a cellular nature, each cell being a pollen grain. Two protuberances, one on each side of the shield or column, represent staminodes. In comparing this flower with the typical monocotyledonous type with six stamens in two whorls (e.g. Tulip), we see that the two staminodes occur in the inner whorl (a third staminode being entirely suppressed) and the functional stamen described above is the only one remaining of an outer whorl of three stamens. In the *Orchidaceæ*, therefore (with few exceptions), the andrœcium has been reduced to

Fig. 71. ***Orchidaceæ. Orchis maculata.*—A, median section of flower; axis on right and bract on left; note parietal placentæ bearing the numerous minute ovules. B transverse section of ovary showing branched parietal placentæ and ovules. C floral diagram; note correct orientation of spurred labellum; floral formula, $[P_{3+3}(A_1G_{(\bar{3})})]$.**

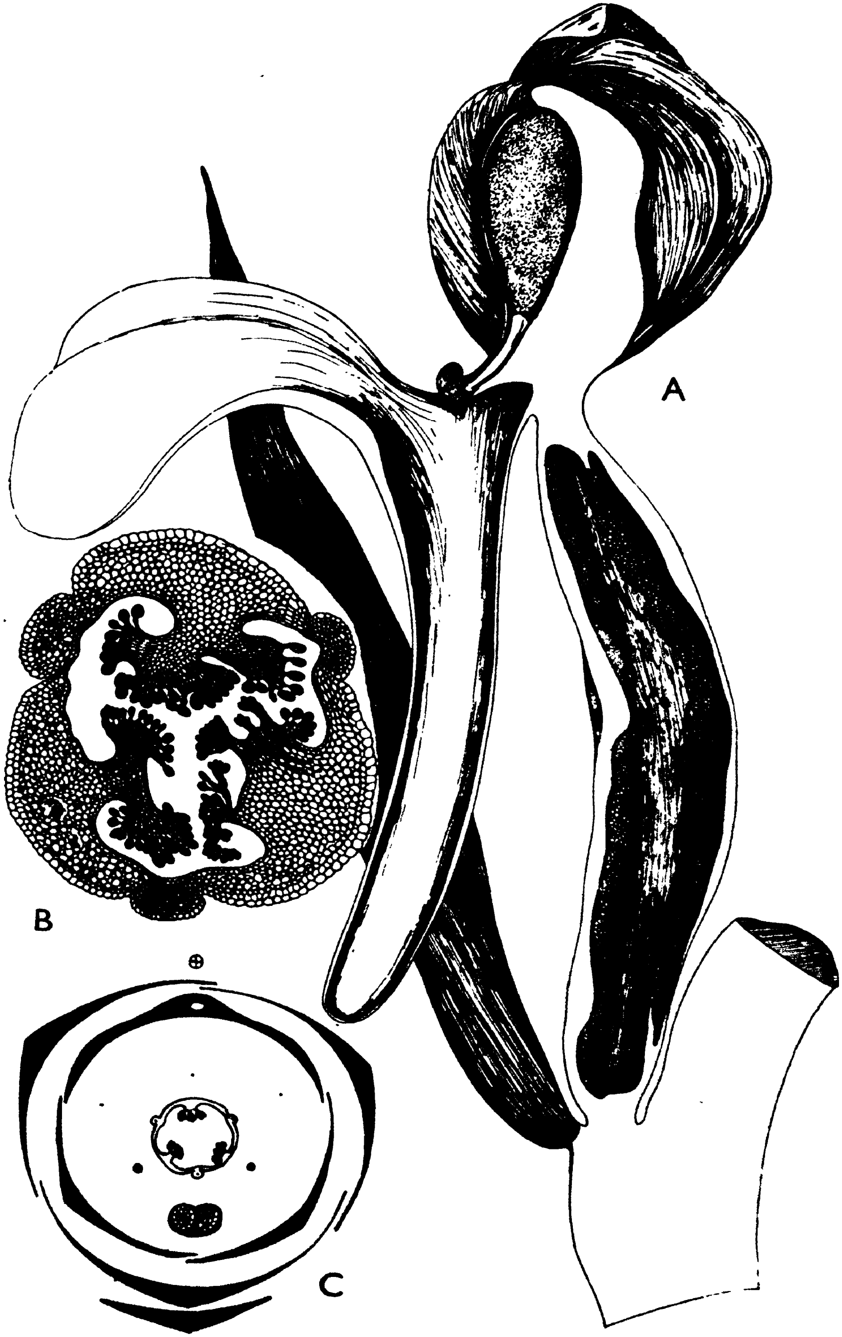

Fig. 71. (For description, see opposite)

the minimum, but notwithstanding this reduction, the mechanism of cross-pollination is probably the most elaborate and efficient of any flowering plant.

Gynœcium: three carpels, syncarpous, inferior. The torsion in the ovary affects the whole orientation of the flower. Up to a comparatively advanced stage of development (fig. 69) there is no twist in the ovary, and the labellum with its spur prolongation *faces the axis* (fig. 69, A and B). The true position of the labellum is, therefore, *posterior*. With further development, however, the tissues of the ovary-wall are stimulated to unequal growth in such a way as to cause the ovary to twist through 180 degrees. This new position permanently alters the orientation of the floral members so that the labellum appears to be facing the bract, and, therefore, falsely anterior. The torsion has the effect of bringing the orifice of the spur, the shield with its pollinia, the rostellum and adjacent stigmatic areas, all to full exterior view.

The labellum is broadly attached around the base of the column and just below the rostellum it becomes deeply recessed. The recess is continued into the narrow spur; the stigmatic areas are situated to the right and left of the orifice of the spur above which hangs the projecting rostellum cup. The latter is considered to be a third, aborted stigma. The unilocular ovary is furnished with three parietal placentæ, which are ridged and corrugated (fig. 69, D). Ovules are not laid down until pollination is effected; they are very small but are developed in enormous numbers (fig. 71, A and B).

Pollination: the flowers are visited by bees which use the labellum as a landing platform and puncture the succulent tissue lining the spur for the sweet juice. While the insect is drilling into the spur, the pressure of its head against the rostellum-cup breaks the thin covering-membrane and causes the gummy contents to exude. This action exposes the discoid bases of the pollinia, and the gummy discs are thus pressed on to the insect's head. In the brief interval before the insect withdraws from the flower the gum sets hard like cement, and one or both pollinia may thus be dragged out attached to the bee's head. The action of the insect may be imitated by thrusting a sharp-pointed pencil into the spur, or the rostellum itself may be directly stabbed; on withdrawing the pencil with one or both pollinia attached, it will be observed that the pollinia stand quite erect, but soon bend forward at right angles to their caudicles and diverge slightly from each other. In this position, if the pencil is now inserted into the spur, the masses of pollen will strike against the sticky stigmatic surfaces to the right and left of the median rostellum (hence the divergence of the pollinia); some of the pollen masses may be torn off and retained when the insect flies away with the rest of the pollinium; one pollinium may thus serve to fertilize a number of flowers. In the absence of insect-visitation pollination is impossible in this species.

Fruit: a capsule opening along the dorsal sutures. The seeds are formed in enormous numbers and are so small and light that they are easily dispersed by wind. The successful germination of Orchid seeds is a matter of some difficulty, and in nature a high percentage of the seedlings perish. This failure is not due to any inherent lethal factor but probably to the precarious chances of the seedlings becoming infected with the mycorhizal element without which the absorptive functions of the plant are impaired. In the absence of such fungal infestation at the seedling stage the young plants make little headway and perish.

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GLOSSARY

Adnate, organs of different nature fused together, e.g. portion of leaf-stalk and stem (p. 205).

Adventitious, arising from unusual position, e.g. branch-roots from stem or leaf.

Aerial roots, roots arising above ground (p. 248).

Allelomorphs (Allels), the alternative factors that separate out in Mendelian inheritance (p. 111).

Anastomosis, union of cell-fibres, e.g. within hypodermis of anther.

Apical meristem, the young, undifferentiated growing tissue at the top of any axis, e.g. growing point of a shoot.

Apogamy, development of an embryo without sexual reproduction.

Apomixis, development of an embryo from the diploid tissue of the nucellus intruding into embryo-sac (p. 95).

Archesporium, the tissue which gives rise to spores (p. 60).

Aril, see *Caruncle.*

Asexual, see *Vegetative propagation*

Axil, angle between a leaf or bract and the stem.

Bivalent, a pair of chromosomes (p. 68).

Bract, a small leaf in whose axil a flower arises.

Bracteate, bearing bracts or resembling a number of green or brown bracts.

Bracteole, a small bract on the stalk of a flower.

Callus, tissue formed to heal a wound.

Caruncle, a hard, oil-containing body on the testa of a seed, close to the micropyle (p. 94).

Centromere, a small point of fixed location in a chromosome by which it becomes attached to the nuclear spindle (=attachment constriction) (p. 56).

Character, any plant attribute, especially in reference to heritable properties, e.g. height, colour. It is the expression of a particular factor in a particular genetic and physiological environment.

Chiasma, the visible consequence of " crossing-over " in the chromosome pair (p. 66).

Chlorophyll, the green colouring matter of plants.

Chromatid, the longitudinal half of a chromosome (p. 56).

Chromatin, the substance of the chromosomes.

Chromomere, one of the small bead-like particles appearing along the length of a chromosome (p. 56).

Chromosome, a body within a nucleus which divides at cell-division ; it carries the hereditary genes.

Cleistogamy, the production of small flowers which never open and are habitually self-fertilized (p. 84).

Coleoptile, the sheath protecting the young leaves and growing-point of a monocotyledonous embryo (p. 95).

Coleorhiza, the root-sheath of a monocotyledonous embryo (p. 95).

Connate, similar parts fused together, e.g. a pair of opposite leaves at their bases.

Cotyledon, seed-leaf.

Cytoplasm, the living contents of a cell, excluding nucleus.

Definitive nucleus, that derived from fusion of the two polar nuclei in embryo-sac; it takes part in the triple fusion resulting in the formation of endosperm (p. 86).

Dichogamy, ripening of stamens and carpels at different times.

Dicotyledon, a flowering plant with two seed-leaves (cotyledons).

Diploid, having the two members of a pair of chromosomes; the normal vegetative or somatic condition of the nucleus.

Dorsal, near the " back "; opposite the ventral side.

Endocarp, the inner limits of the wall of a fruit (p. 98).

Epicarp, the outer skin of a fruit.

Epidermis, the outermost layer of covering cells.

Exine, the outer wall of a pollen grain (p. 70).

Factor, a hereditary unit, also called a *gene.*

Fibre, a long, thick-walled cell, usually lending support to thin-walled cells.

Fibrous, having thick, hard strands lining a cell-wall for support or reinforcement.

Gamete, a sexual cell, male or female (p. 86).

Gene, a hereditary unit (see *Factor*).

Haploid, having one from each pair of chromosomes (half the vegetative or somatic number) as in the gametes (p. 62).

Heterotype, the stage of reduction at meiosis where the chromosomes are half the number (p. 64).

Homotype, nuclear division resulting in same number of chromosomes as before; ordinary nuclear division (p. 64).

Hyphæ, the filaments of a fungus.

Hypodermis, the layer of cells immediately below the outer epidermis.

Indefinite, continued development from the growing point.

Intine, the thin inner wall of the pollen grain (p. 70).

Involucre, the collection of bracts closely aggregated around the base of an inflorescence.

Lamina, the flat blade of a leaf.

Liane, a woody climbing stem of tropical forests.

Loculus, the cavity within an ovary.

Macrosporangium, the integuments of the ovule together with the nucellus, surrounding the macrospore.

Macrospore, embryo-sac.

Megaspore, see *Macrospore.*

Meiomery, condition of having less than the normal number of parts (p. 50).

Meiosis, nuclear division resulting in production of half the number of chromosomes, as in gametes (p. 62).

Mericarp, portion of a splitting (schizocarp) fruit (p. 99).

Meristem, the young, actively dividing cells of any tissue, especially those of growing points.

Mesophyll, internal tissue of a leaf.

Microsporangium, pollen-sac.

Microspore, pollen grain.

Mitosis, ordinary nuclear division resulting in the same number of chromosomes as before (p. 58).

Monocotyledon, a flowering plant whose seeds have one seed-leaf (cotyledon).

Mother-cells, cells which form spores.

Nectar, a sweet substance secreted by glands, especially glands in the flower.

Nectary, glandular tissue secreting nectar.

Nucleolus, a small opaque body embedded in the nucleus, of doubtful function.

Nucleus, the body in a cell which harbours the chromosomes.

Octant, the eighth part of a spherical cell, e.g. the embryonic cell (p. 90).

Ovary, the part of a carpel enclosing one or more ovules.

Ovule, the body, containing the ovum, which after fertilization becomes the seed.

Papillose, covered evenly with small lumps.

Parthenogenesis, development of embryo from ovum without fertilization by a male gamete (p. 95).

Periblem, the young tissue at the growing-point which gives rise to the cells between the epidermis and the vascular tissue, i.e. the cortex.

Pericarp, wall of the fruit (p. 96).

Perisperm, tissue in a seed derived from the nucellus.

Photo-synthesis, formation of starch by a green plant in the light.

Pistil, the ovary or gynœcium.

Pleiomery, condition of having more than a normal number of parts (p. 52).

Plerome, the young tissue at the growing point which gives rise to vascular tissue.

Primordium, small lump of undifferentiated tissue which develops into any specified organ.

Proboscis, the nectar-sucking organ, as of an insect.

Prophyll, see *Bracteole.*

Radicle, the young main root.

Reciprocal-crossing, cross-pollination in two ways, with either of the two plants concerned as pollen parent.

Soma, the vegetative plant considered as distinct from its strictly sexual reproductive parts.

Somatic, referring to the vegetative parts of a plant, apart from the reproductive.

Spathe, a large protecting bract enclosing the flower or inflorescence, especially of Monocotyledons.

Stipules, a pair of small leaves, tendrils, or spines, at the base of the leaf stalk. (*Exstipulate,* with no stipules.)

Stolon, horizontally growing stem rooting at the nodes.

Stoma, one of the breathing pores in the epidermis, especially of the leaf.

Ternate, of three parts, e.g. a compound leaf of three leaflets.

Tetrahedral, like a three-sided pyramid with a convex base.

Vascular strand, a vein; the xylem and phloem.

Vegetative bud, one which forms stem and leaves.

Vegetative propagation, growth from division of any part of a plant to produce a separate individual, without sexual reproduction.

Ventral, lower (surface).

Whorl, a ring of members at the same level.

Xerophyte, a plant adapted to withstand drought.

Yield, weight of a crop, as of seeds, hay, &c.

Zygote, the fertilized ovum which develops into an embryo (p. 86).

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